NONRANDOM EXTINCTION AND THE EVOLUTION AND CONSERVATION OF CONTINENTAL MAMMAL FAUNAS

By

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I investigated extinction processes and their applications to the the study and conservation of mammals. I found evidence that nonrandom extinction explains part of the pattern of associations among the variables, population density, geographic range size and body size, for North American mammals.

I then posited that if extinction can explain associations among variables, then we ought to be able to use associations among variables to make predictions about extinction. Using data for North American (north of Mexico) and Australian mammals, I developed a method to predict which species not currently threatened with extinction are most likely to become so in the near future.

I then sought ways to predict extinction over much longer spans of time, by combining several of the features of existing theories of extinction into a shotgun/logistic model of adaptive radiation and nonrandom extinction. In this model, adaptive radiation is a wasteful process that produces many species, most of short duration. However, the few species resulting from the subsequent species selection are generally, more *K*-selected, poorer colonists and more specialized in a number of respects; but they are less prone to extinction except during periods of environmental disturbance. I then assessed the validity of assumptions of the shotgun model and tested predictions derived from it.

My general conclusion was that knowledge of patterns of extinction were useful for 1) the study of relationships among several variables; 2) prediction of species endangerment; and 3) the study of evolutionary trends. Extinction might thus be considered as a common currency for the disciplines of conservation, ecology and evolution. Paradigms developed by workers in each of these fields can sometimes be modified to apply to the others as well, resulting in a useful framework of study.

CHAPTER I
THE IMPORTANCE OF NONRANDOM EXTINCTION--AN INTRODUCTION BY EXAMPLE

Introduction

The concept of species selection has a venerable history (Grant 1989). Although various authors have coined their own terms (e.g., differential extinction and natural selection at the level of species) to encompass only certain aspects of the process, all probably agree on the basic process involved. Nevertheless, in some ways, species selection is a more difficult process to study than is natural selection. Investigators of natural selection can frequently identify the agents responsible for differential reproductive success among individuals, but investigators of species selection can rarely do so. In this dissertation I posit new ways to uncover species selection that derive from knowledge of extinction. This investigation will take the form of a series of predictions, the explications of which are found in the text of the dissertation. Although these predictions will probably make little sense to the reader at present, he or she may find it easier to keep track of them by referring to Table 1-1. A prediction can be located in

Table 1-1. Predictions explicated in Chapters I, IV, V and VI.

1.1[*] The RS / density correlation for size-restricted mammals should be more positive than the correlation for mammals of all sizes.

1.2 The correlation between RS and density for Australian mammals will be intermediate in strength or direction between those for North American birds and North American mammals.

1.3 When body size is controlled, any association between RS and density will no longer be significant.

1.4 When both direct and indirect influences of size are controlled, the association will no longer be significant.

1.5 Body size will be the most important independent variable in a regression with density as dependent variable, whereas density will be the most important variable in a regression with RS as dependent variable.

4.1a Stratigraphic range and RS will have large variances among the species within a genus.

4.1b Litter size and HBL will have smaller intrageneric variances than stratigraphic range and RS.

4.1c Length of lactation will have a smaller intrageneric variance than the above-mentioned variables.

4.2 Variation among monospecific genera is similar to that among speciose genera when intrageneric variation is controlled statistically.

4.3 Signs of association will tend to differ among taxonomic levels, and the differences will be greater with widely-disparate levels than among taxa that are fewer levels apart.

5.1 Monospecific genera will have greater stratigraphic ranges than species from speciose genera.

5.2 Monospecific genera have more unusual characteristics than species from speciose genera.

Table 1-1--continued.

5.3 Variables for monospecific genera will differ from species in speciose genera in the same direction that K- strategist species differ from r- strategist species.

6.1 Species of mammals that are able to expand their geographic ranges during a period of disturbance are expected to be r- strategists relative to species whose ranges remain stable or shrink during disturbance.

6.2 Endemics should experience high extinction rates during periods of great environmental change.

6.3 Colonist species should make few successful incursions into old and climatically stable habitats.

6.4 With time, K- selection will transform colonists into specialized endemics.

*Predictions are explicated in the chapter denoted by their number. For example, Prediction 6.1 is the first prediction elaborated in Chapter six.

the text by referring to the chapter denoted by its number. For example, Prediction 4.2 is the second prediction described in Chapter IV.

In this first chapter I will investigate whether the associations among certain variables are most readily explained as being due to species selection. In the next chapter I will shift emphasis from comparing variables to comparing groups of species that differ in attributes, in order to develop a specific application of extinction theory to conservation. In subsequent chapters I will elaborate the concept that the attributes of species can be used to predict extinction, but I will extend the investigation into the distant past.

As a first principle, I considered that since species selection requires the extinction of species, it is almost axiomatic that species selection will be most readily detected when there have been many extinctions of species. A corollary assumption is that no selective agent should be invoked if the species becoming extinct were a random subset of the biota. There is a large body of work supporting the contention that there is a strong deterministic component to the extinction process, and that the species most likely to become extinct differ in attributes from those less likely to perish. I therefore list only a few examples, including Guilday (1984); Brown (1971, 1984); Brown and Maurer (1986); Anstey (1978); Hansen (1980, 1982); Vrba (1980); Jablonski and Lutz (1983); Ward and Signor (1983); Cassels (1984); Guthrie (1984); Horton (1984); Kiltie (1984); McDonald (1984); Murray (1984); Trotter and McCulloch (1984); Webb (1984); Heaney (1986); Knoll (1986); Lawlor (1986); Morgan and Woods (1986); Moulton and Pimm (1986); Patterson and Atmar (1986); and Brown and Maurer (1987). Herein I consider valid the assumption that the extinction of species with certain attributes is implicated in species selection.

In the first chapter I posited that it is easier to detect species selection among the associations of some variables than among others. Using published information on North American land mammals, I concentrated on three variables. One of these was body size, manifested in this study by head-and-body length (HBL). The other variables investigated were density, expressed as number of individuals per hectare; and geographic range size (hereafter designated as RS), expressed in $km^2 \times 10^{-2}$. I chose these three variables because there were some hints that species selection is especially appropriate in explaining the pattern of associations among them. Several other variables were also included in some analyses, but they did not play an important part in this investigation. Data from Australian mammals were also used to assess associations among variables, although more detailed investigations were considered impractical because of small sample sizes.

I considered RS to be an especially interesting variable for several reasons. RS varies far more among North American mammals than many other variables, such as gestation period (Appendix B). Furthermore, this variation is nearly as great at lower taxonomic levels as at higher levels. This is exemplified by such genera as *Peromyscus*, *Microtus*, *Reithrodontomys*, and *Spermophilus*, and (in recent history) by the genera *Canis* and *Mustela*. It seems likely that diverse and interesting factors affect RS. Table 1-2 lists some of these variables. One of the most intriguing of these is the second variable of special interest, body size. Body size differs between taxonomic levels in sign of association with RS. Furthermore, the range of body size differs greatly between birds and mammals, two classes that will be shown below to differ in another, perhaps related aspect. That aspect involves the third variable of interest, population density (hereafter simply referred to as density). Although most studies have indicated a positive association between density and RS (e.g., Bock and Ricklefs 1983; Brown 1984; Brown and Maurer 1987), theoretical considerations led me to doubt the generality of this assertion. Referring to Table 1-2, we can see that RS has been suggested to correlate positively with both density and body size. Since body size and density have the same sign of association with a third variable, we might expect them to correlate positively with each other.

Table 1-2. Sign of association of various variables with RS.

Variable*	Sign of Association	Sources
Mean Litter Size	+	Glazier (1980)
Maximum Litter Size	+	Glazier (1980)
Animalivory	+	Hesse *et al*. (1937); Anderson (1977); Rapoport (1982)
Area of Land Mass	+	Hesse *et al*. (1937); Flessa (1981); Anderson & Koopman (1981); Brown & Maurer (1987)
Use of Marginal Habitats	+	Baker (1968)
Eurytopy	+	Baker (1968); Stanley (1979); Glazier (1980)
Number of Sympatric Congeners	-	Glazier (1980); Mace & Eisenberg (1982)
Longevity	-	Glazier (1980)
Body Size (w/in Genus)	-	Glazier (1980)
Body Size (w/in Class)	+	VanValen (1972); Anderson (1977); Rapoport (1982)
Maximum Reproductive Potential	+	Glazier (1980)
Reproductive Effort	+	Glazier (1980)
Age at First Reproduction	-?	Glazier (1980)
Species Richness of Genus or Family	+	Rapoport (1982)
Number of Subspecies/ Species	+	Rapoport (1982)
Population Density	+	Bock & Ricklefs (1983); Brown (1984)
Colonizing Ability	+	Dwyer (1978); Stanley (1979); Glazier (1980)
Vagility	+	Hesse *et al*. (1937); Anderson (1977); Glazier (1980)

Table 1-2--continued.

Variable*	Sign of Association	Sources
'*r*-selected' Traits	+	Carlquist (1965); MacArthur & Wilson (1967); Diamond (1974, 1975); Boucot (1975); Glazier (1980)
Encephalization	+	Mace and Eisenberg (1982)
Diversity of Fauna	-	Rosenzweig (1975)
Dietary Breadth	+	Hesse *et al*. (1937)

*The qualitative designations "+" and "-" are used to describe all associations because several of the cited references did not quantify relationships among variables studied.

However, empirical studies on mammals have reported density and body size to correlate negatively (e.g., Eisenberg 1981; Peters 1983; Robinson and Redford 1986). Thus RS is a rather whimsical variable that defies understanding by reference to bivariate associations alone.

One possible explanation for the anomalous signs of association among density and RS is that the relation is spurious, such that the association would disappear when a third variable is controlled. I reasoned that body size was the variable most likely to influence the correlation between RS and density. My rationale for this comes largely form Brown (1981) and Brown and Maurer (1987), although they might not agree with my interpretation. My reasoning is as follows.

Large species tend to reach lower densities than do smaller species for reasons dictated by energetic constraints. Since individuals of large species of endotherms use absolutely more energy than do individuals of small species of endotherms, a given unit of area generally can support more individuals of small than of large species of mammals. Density is simply the number of individuals per unit area or volume; hence, when individuals are large, there will be fewer individuals in the same area and their density will be lower.

Furthermore, large species of the same RS as small species should have smaller population sizes. Since population size correlates inversely with probability of extinction, large species with the same RS as small species will have a greater probability of extinction than will small species. Thus, in general, small species should be able to survive with smaller RS than will large species. Over long periods of evolutionary time, this should result in a paucity of large species that have small RS; and hence, an overall negative correlation between density and RS. However, small species can survive in either small or large RS; hence, the overall correlation between RS and size, though positive, is rather weak.

If this body-size-dependent process is the only one tending to produce a negative association between RS and density, then controlling for body size should eliminate a negative correlation. Furthermore, since the variation in body mass of North American mammals is nearly two orders of magnitude greater than that for birds, this process should be more important for mammals than for birds. I hypothesized that if the analysis for mammals were restricted to a size range similar to that in a study of the correlation between RS and density in birds, then the correlation for the mammals would be more similar to that for birds than would an overall analysis with mammals of all sizes. Since the RS/density correlation for birds is positive, then Prediction 1.1 was that the RS/density correlation for size-restricted mammals should be more positive than the correlation for mammals of all sizes. I also suspected (Prediction 1.2) that since the range of body sizes of Australian mammals is intermediate between that of North American birds and North American mammals, the associations between variables would be intermediate in strength or direction.

To test Prediction 1.1 I undertook tests of association for North American mammals as a whole and then for mammals less than 160 mm head-and-body length (HBL). Although this analysis will be discussed further below, for the moment I will mention that it was consistent with my hypothesis. The analysis was not, however, particularly satisfying. One reason to doubt the generality of the analysis on small mammals was that it used slightly fewer species than an analysis using mammals of all sizes; hence, the lack of significance could simply have been due to a smaller sample size. Furthermore, if the test was nonsignificant but nevertheless indicated a negative association, the suspicion could always be entertained that a larger or more accurate data set would yield a significant result.

I therefore undertook more quantitative and objective regression analyses that included all the North American nonvolant species of mammals, but that statistically controlled for HBL. One way to control for a variable that can be interpreted visually is to separately regress the two variables in question against the variable to be controlled, then to plot the residuals of both regressions against each other. This double residual plot can then be inspected for trends. I was particularly interested in the slope of these plotted residuals; a negative slope on a plot of the residuals of the RS regression vs. the residuals of the density regression would indicate that density and RS are still negatively correlated even when HBL is controlled. This subjective assessment can then be followed by a regression that includes all three variables simultaneously, to more objectively quantify the strength and significance of relationships among variables when others are controlled. Hence, Prediction 1.3 was that if body size is controlled, the association between RS and density would be nonsignificant.

However, body size is such a pervasive variable that it could have indirect effects on density or RS by affecting other variables that in turn influence density or RS. Although one of the requirements for statistical analyses is that the sample is random, living species are themselves a nonrandom set of all species that have lived or could possibly live. Since evolution is not the result of natural selection on each character of an organism in the absence of all other characters, it is inevitable that characters will sometimes be so subtly linked as to elude attempts at perfect statistical control. Complete statistical control would require an assessment of all the indirect effects of size that result from the association of the variable in question with other variables that are influenced by size. Thus there was always a possibility that the effect of body size was still not completely removed, despite my attempts to do so by statistically controlling HBL. Hence, I included in the model three other variables that were known to correlate significantly with HBL, in the hope that controlling for their influence would simultaneously eliminate most of the indirect influences of body size. I reasoned that if the association was still significantly negative after both the direct and indirect influences of body size were removed from the model, then some process other than size-dependent species selection has been at work to produce a negative relation. Prediction 1.4 was thus that controlling for the combination of direct and indirect influences of HBL would eliminate the significant correlation between density and RS.

I was then ready to investigate the sequence of cause and effect events. Heretofore in the regression analyses I undertook, I had somewhat arbitrarily specified density as the dependent variable. Although disentangling cause and effect relationships among variables is difficult, the primacy of body size as an ecological variable suggested that it should be considered an independent variable in the model. Of the variables RS and density, the latter seemed to be the most directly influenced by the independent variable, body size (HBL). By contrast, I posited RS to be affected by body size only indirectly, through density. As an example, consider species of small RS and at low density, which have a relatively high probability of extinction. If species of large body size have low density, then they are likely to be extinction-prone in small RS. Thus there could be an overall correlation between RS and body size, simply because both of these variables are correlated with the intermediate variable, density.

I reasoned that if this purported chain of causation is correct, then the associations between variables should be strongest among a pair of variables whose members are directly linked, than among a pair whose members are only linked via an intermediary variable. Regression of Y on X is not in general the same as regression of X on Y (Sokal and Rohlf 1973), especially when there is more than one independent variable. Hence, when variables switch from being considered dependent to independent (or vice versa), there could be different results. Thus a regression with RS as dependent variable and density and HBL as independent variables, could yield different associations than one specifying density as dependent variable and the other two variables as independent variables. Prediction 1.5 was that body size would be the most important independent variable in a regression with density as dependent variable, whereas density would be the most important variable explaining RS in a regression with RS as dependent variable.

Materials and Methods

Initially I chose North American mammals for my subjects because of my familiarity with the taxa and because natural history information was available for many species. I did not undertake analyses for North American bats for several reasons, not the least of which was lack of data for densities. Data for Australian mammals was used in a more perfunctory manner.

Using data for North American mammals only, I created models using log transformed data for the variables gestation period (in days), home range size (in hectares), and litter size, were also created to test the possibility that they might eliminate the negative association between RS and density.

The Variables

Head-and-body length (HBL) information was available for all but one species. Gestation period (in days) information was available for 130 species. Gestation periods of species with delayed development were not recorded or used in the analysis, not only because the variance would increase greatly but also because the occurrence of delayed development tends to follow phylogenetic lines rather than the ecology or behavior of the species. For example, mustelids of diverse habits have delayed development, whereas the opossum *Didelphis*, like all marsupials, has a short gestation period.

Density information was available for more than the 97 species shown in my data set. However, certain species with extremely variable densities (e.g., the lemmings *Dicrostonyx* and *Lemmus*) were excluded because their calculated means are difficult to interpret biologically.

Since this study concentrated on the implications of RS, only species were included for which RS information was available. This was not an important limitation because RS data were available for almost all North American species. The baseline RS values for both North American and Australian mammals were provided by Dr. Sydney Anderson of the American Museum of Natural History in New York City. However, Dr. Anderson's estimates are for RS within the continent of North America, and I felt that the RS values used in my analysis should refer to the total RS for the species. Therefore I measured the extralimital RS of species which also live in Eurasia or South America and added them to the North American values. For species found also in Eurasia I used maps from Corbet (1978) and Burton (1979); for species found also in South America I used maps made by Dr. Ralph Wetzel and provided for me by Dr. John Eisenberg. To measure areas I drew the contours of these maps by eye onto standardized photocopies of maps of Eurasia and South America, then estimated the areas on my maps with a compensating polar planimeter. Although the margins for errors in these estimates of RS are high, the ranks of RS are probably more nearly correct because of the large variance of RS among species. All units are expressed in units of $km^2 \times 10^{-2}$.

Clearly the RS of a species could change because of anthropogenic activities and thus automatically alter its relation to other variables that remain more constant. In practice, however, the range maps found in most texts depict a primitive, unfragmented range, such as might be attributed to natural forces of evolution. The range maps from which my RS data were calculated depict these unfragmented geographic ranges. Hence, they are suitable for studies of evolution and species selection.

The Data Set

The primary data sets for mammals used in this and subsequent chapters are presented in Appendices A-F. Published sources of data for North American mammals included, in addition to those mentioned previously, Armstrong and Jones (1972); Baker and Schump (1978a, 1978b); Beckoff (1977); Bednarz (1977); Best (1986); Best and Lackey (1985); Birkenholz (1972); Bleich (1977); Case (1978); Carraway and Verts (1985); Carroll and Genoways (1980); Chapman (1974, 1975a, 1975b); Chapman and Feldhammer (1981); Chapman *et al*. (1982); Chapman and Willner (1978; 1981); Clark *et al*. (1971, 1987); DeMaster and Stirling (1981); Dolan and Carter (1977); Dowler and Genoways (1978); Egoscue (1979); Ernest and Mares (1987); Eshelman and Cameron (1987); Franzmann (1981); French (1980); Fritzell and Haroldson (1982); Galbreath (1982); Gardner (1982); Getz (1985); Godin (1977); Green and Flinders (1980); Hallett (1978); Heaney (1984); Hillman and Clark (1980); Hoffmann and Owen (1980); Hoffmeister (1986); Howard and Marsh (1982); Ingles (1965); Jenkins and Busher (1979); Jenkins and Eshelman (1984); Jones et al. (1983, 1985); Kaufmann (1982); Keller (1985); King (1983); Kirkland (1981); Kirkland and Jannett (1982); Lent (1988); Limm (1987); Linzey and Packard (1977); Long (1974); Ludwig (1984); MacDonald and Jones (1987); Maser et al. (1981); McCallister and Hoffmann (1988); McCarty (1975, 1978); McGrew (1979); Meagher (1986); Mech (1974); Merritt (1981, 1987); Michener and Koeppl (1985); Murie and Michener (1984); Nadeau (1985); Nash and Seaman (1977); O'Farrell and Blaustein (1974a, 1974b); O'Gara (1978); Oaks et al. (1987); Owen (1983, 1984); Paulson (1988); Peek (1982); Pembleton and Williams (1978); Pizzimenti and Collier (1975); Pizzimenti and Hoffmann (1973); Powell (1981); Richart (1987); Rideout and Hoffmann (1985); Shackleton (1985); Shellhammer (1982); Smolen and Keller (1987); Snyder (1982); Streubel and Fitzgerald (1978a, 1978b); Sullivan et al. (1986); Tamarin and Kunz (1974); Tim (1985); Verts and Carraway (1987a, 1987b); Webster et al.

(1985); Whitaker (1972, 1974, 1980); Whitaker et al. (1972); Williams (1982); Williams and Baker (1974); Wolf (1982); Woods (1973); Young and Jones (1982); and Zegers (1984). John Eisenberg also provided unpublished information on heteromyids. The nomenclature is as in Hall (1981), with some minor changes, shown below. These names reflect changes suggested by taxonomists subsequent to the publication of Hall (1981). For comparative purposes mice of the genus Peromyscus were excluded from this analysis. By excluding Peromyscus I assured that my data were independent and comparable to Glazier (1980), who did a somewhat similar analysis for that genus.

Name Used Herein	Name in Hall (1981).
Sorex monticolus	Sorex vagrans
Sorex pacificus	Sorex vagrans
genus Tamias	genus Eutamias
Marmota broweri	Marmota caligata

Variation in values was considerable for some species. I used arithmetic means whenever possible; even when the literature presented maximum and minimum values for a variable, I used the midrange. When data for more than one subspecies were provided I first calculated means for each subspecies, then calculated the mean of those values. When data for both sexes were provided, I found the means for each sex and then the mean of those two values. There were many missing values. These were simply ignored by the computer analysis. Although specialists could probably have provided information to fill in some of these blanks, the time necessary to obtain the most complete data for every species was prohibitive. Several variables in the appendices had small sample sizes or were not useful for other reasons. These will not be discussed further or will be mentioned only briefly.

Most of the Australian data are from Strahan (1983), with additional information from the following sources: Aslin (1975a, 1975b); Aslin and Watts (1980); Barnett et al. (1977); Begg et al. (1983); Braithwaite (1983); Braithwaite et al. (1984); Breed (1979); Caughley (1986); Christensen et al. (1984); Cockburn (1981); Fanning (1982); Fleming and Frey (1984); Floyd (1980); Friend (1987); Gall (1980); Jarman and Taylor (1983); Johnson (1987); Johnson and Jarman (1987); Johnson (1980); Johnson (1979); Kaufmann (1974); Kerle (1984); Merchant et al. (1984); Morton (1978); Nelson and Goldstone (1986); Norton (1987); Poole and Merchant (1987); Read (1987); Rose and McCartney (1982a, 1982b); Russell (1986); Short et al. (1983); Smith (1979); Southwell (1987); Suckling (1984); VanDyck (1979); Wells (1978); Wilson (1986); Wilson et al. (1986); Woolley (1984); Woolley and Valente (1986).

Statistical Procedures

Statistical procedures are described in Agresti and Agresti (1979). Kendall's tau-b correlation, available in the SAS statistical package (SAS Institute 1985) was the measure of association used for exploratory tests of associations. Nonparametric tests such as tau-b are far superior to parametric tests for data that exhibit nonnormal distibutions or heterogeneity of variance, such as occurs in several of the variables in my data set. Tau-b was especially appropriate for my investigation because it does not require normally distributed variables and can make use of either interval or ordinal variables. Although very versatile, tau-b is sensitive to small sample sizes (Agresti and Agresti 1979). Sample sizes for my analyses were, however, adequate.

I did not undertake tests of association for North American birds because this information is already available in the published literature (Bock and Ricklefs 1983). To test my hypothesis about the RS/density anomaly (Prediction 1.1), I ran the North American analysis again but included only mammals in approximately the same size range as the birds (HBL < 160 mm).

My second approach to correcting for body size was to regress the log of each variable separately on the log of HBL (log transformations were necessary because the raw data for the variables were not linearly related). Then I plotted the residuals of each regression against the other. If size accounts for all the significant variation in either variable, then a double residual plot should exhibit a random scatter of points. Conversely, if the plotted residuals tend to indicate either a positive or negative slope, then RS and density will probably be found to be significantly associated even when the effects of HBL are removed. To test Prediction 1.2 I undertook a tau-b correlation of the variables density and RS for Australian mammals.

To test Prediction 1.3 I included all three variables in a single model. The first regression was of density on RS and HBL. I undertook regressions with both log and rank transformations, although the results of the two were very similar.

To control for indirect effects of size on RS and density (Prediction 1.4), I included in the model log transformed data for the three variables home range size (in hectares), gestation period (in days) and litter size. Data were from Appendices A and B. Since these variables also have significant correlations with HBL, their inclusion in the model might be expected to reduce the effects of HBL to nonsignificance. Ideally I would have included all of these variables in a single model in the hope that controlling for all of them together would all but eliminate indirect effects of HBL on density and RS. In reality, this required a larger data set with far fewer missing values for observations than the set available to me. Although the 258 observations in my data set were sufficient for a regression model with three or four variables, it is really too small for analyses that include many variables. Furthermore, since the regression procedure excludes observations with missing values, and since many of my observations were missing one or more value, each variable added to the model greatly reduced the sample size. For example, a model with density as dependent variable and HBL, RS and home range size as independent variables, used a sample size of only 44. Therefore I limited my models to a maximum of four variables.

Prediction 1.5 was tested using a forward selection, stepwise procedure. This procedure begins with a model that includes the independent variable that accounts for the most variation in the model, providing that the association was significant. Successively less important variables are then added to the model until the added variable makes no significant ($\underline{P} < 0.05$) contribution. Stepwise regression has frequently been misused to find subsets of a set of independent variables that are individually important as predictors of the independent variable. Stepwise regression is, however, appropriate for use in analyses such as mine to discern which variables make additional contributions to the prediction of the dependent variable, given that one or more independent variables are already in the model (Chalmer 1987). In my study, one stepwise regression specified density as the dependent variable; the second, RS.

Results

The tau-b correlation of density and RS for mammals as a whole was significant and negative. By contrast, the association for small mammals was weak and not statistically significant. The correlation coefficient was -0.148, and the P-value was 0.2114. The double residual plot in Figure 1-1 does suggest a negative trend, although there is considerable scatter. The correlation between RS and density for Australian mammals was significant and negative (coefficient = 0.163, P = 0.036).

A summary of all the regression analyses is in Table 1-3 and 1-4. The analyses revealed that HBL is responsible for most of the variation in density, but that RS also made a small but statistically significant contribution to the model. When I repeated the analysis using rank transformation of the data rather than a log transformation, the results were almost identical.

Models using rank transformed data for the variables gestation period, home range size and litter size, also reduced but did not eliminate the negative association between RS and density. Furthermore, in all but one case, the forward stepwise regression including home range size as an independent variable, the association was statistically significant ($P < 0.05$).

Figure 1-1. Double residual plot from linear regressions of geographic range size and population density against head-and-body length. Data used in the analyses were natural-logarithmically-transformed values for North American mammals.

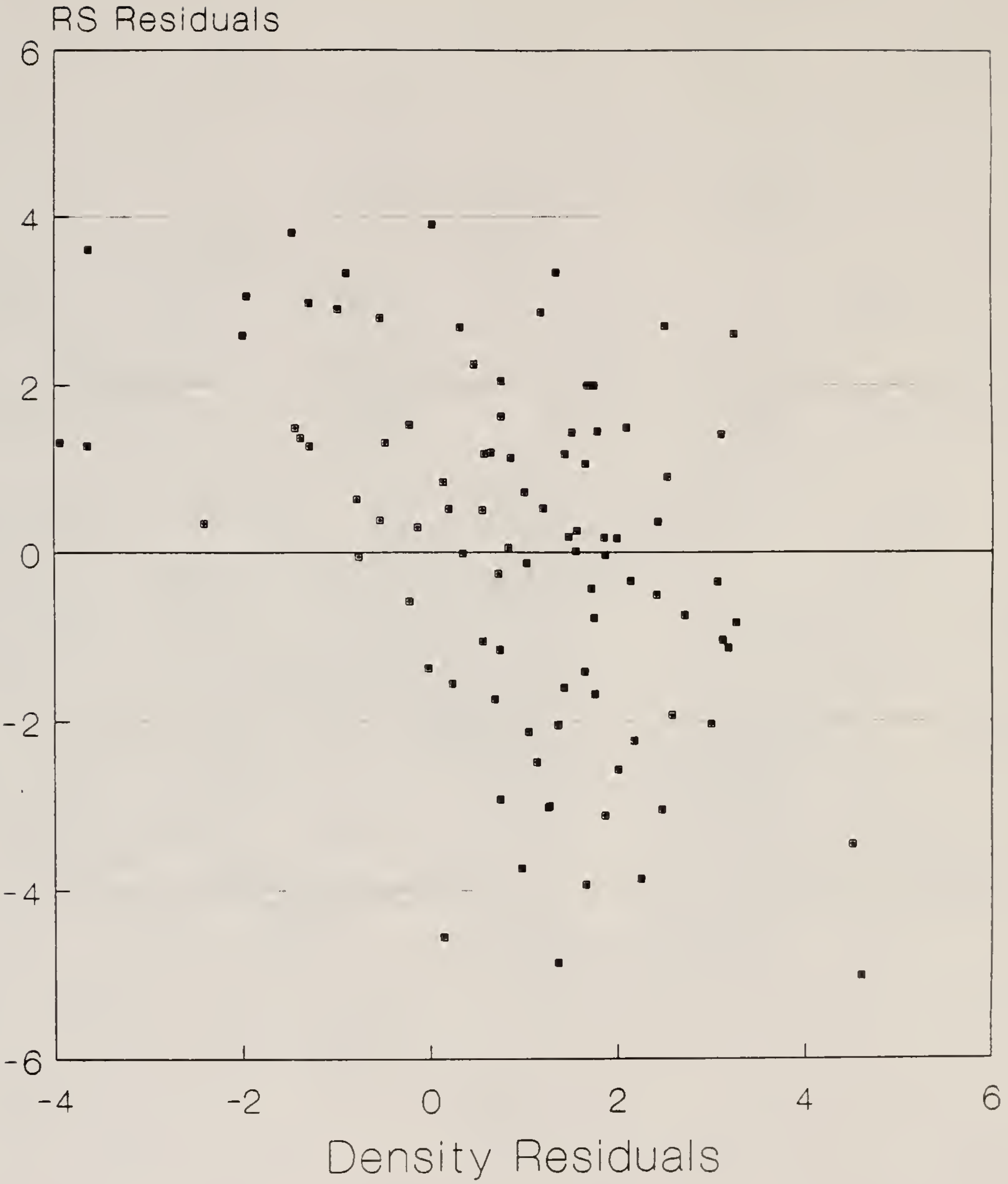

RS Residuals
6
4
2
0
-2
-4
-6
-4
-2
0
2
4
6
Density Residuals

Table 1-3. Summary of linear regressions involving density or RS. Both partial and model correlation coefficients are listed for the final model for the stepwise regressions, but information about the incomplete models is not shown.

Dependent Variable	Independent Variable(s)	Partial R^2	Model R^2	P Value
Log Density	Log RS	-	0.314	0.0001
Log Density	Log HBL	-	0.442	0.0001
Log RS	Log HBL	-	0.191	0.0001
Log Density (stepwise)	Log HBL	0.442	0.442	0.0001
	Log RS	0.127	0.569	0.0001
Log RS[*] (stepwise)	Log Density	0.314	0.314	0.0001
	Log HBL	-	-	NS
Rank Density (stepwise)	Rank Home Range Size	0.744	0.744	0.0001
	Rank HBL	0.018	0.761	0.0909
	Rank RS	0.018	0.779	0.0776
Rank Density (stepwise)	Rank Gestation Period	0.554	0.554	0.0001
	Rank RS	0.040	0.594	0.0134
	Rank HBL	0.004	0.598	0.4074
Rank Density (stepwise)	Rank HBL	0.324	0.324	0.0001
	Rank RS	0.140	0.464	0.0001
	Rank Litter Size	0.028	0.493	0.0247

[*] The second independent variable, Log HBL, made very little contribution ($P > 0.5$) and was excluded from the final model by the stepwise procedure.

Table 1-4. Linear regressions involving density or RS.

Dependent Variable	Independent Variable(s)	Intercept	Slope
Log Density	Log RS	9.9544	-0.9341
Log Density	Log HBL	13.062	-2.2892
Log RS	Log HBL	2.9283	1.1444
Log Density (stepwise)	Log HBL	17.0329	-0.6303
	Log RS		
Log RS (stepwise)	Log Density	10.3142	-0.3362
	Log HBL		
Rank Density (stepwise)	Rank Home Range Size	111.199	-0.1123
	Rank HBL		-0.0872
	Rank RS		-1.8471
Rank Density (stepwise)	Rank Gestation Period	97.1412	-0.5277
	Rank RS		-0.0993
	Rank HBL		0.0425
Rank Density (stepwise)	Rank HBL	95.8067	-0.1629
	Rank RS		-0.1813
	Rank Litter Size		0.0817

As predicted, the stepwise regressions indicated that HBL was better than RS as a predictor of density, and that density was a better predictor of RS than was HBL. However the nonsignificance of HBL in the latter model was rather surprising.

Discussion

Consistent with my model, the correlation between density and RS was most negative for North American mammals, intermediate for Australian mammals, and most positive for North American birds. Thus the negativity of the association increases with range of body size, a result consistent with the interplay of two forces. One of these forces is the tendency for natural selection to couple abundance with expansion into a larger RS. The second force is species selection acting to eliminate species of large body size and small RS. Birds have a small range of body size; hence, exhibit a strong positive relation between RS and density. North American mammals exhibit a much larger range of body sizes and have undergone considerable species selection, resulting in a negative correlation. Australian mammals are intermediate between the former two taxa in range of body size and exhibit an association that is less positive than birds but more positive than mammals.

As hypothesized, the strong negative association between RS and density is in part spurious. When HBL was controlled, the association between these variables was greatly weakened. Furthermore, although RS and density are strongly associated in bivariate analyses, a regression with density as dependent variable and two independent variables indicated a minor importance for RS. Thus for mammals, bivariate associations can be very misleading in elucidating the evolutionary interactions among variables.

Although I could not be confident that I completely controlled for all the indirect effects of size, I examined enough variables to greatly reduce such effects. I therefore present as an alternative an entirely different explanation for the negative RS/density association that remains when influence of HBL is removed.

Poor colonization ability as a cause of negative correlation

In accord with published information, I suggest that for most animal classes, not only are RS and density positively correlated, but that RS and colonizing ability are positively correlated. I will concentrate on two attributes of good colonists, namely fecundity and vagility.

The importance of fecundity to colonizing species is a cornerstone of *r*- and *K*- selection theory. Fecundity is probably also important to species colonizing mainland habitats, as exemplified by a simple calculation.

Suppose that the geographic range of a hypothetical species is contained within a circle of radius 10 km_2. The RS of this hypothetical species would then be approximately 314 km^2. If the species were to expand its geographic range to encompass the area within a circle of radius 20 km, it would then have an RS of approximately 1,250 km^2. Thus in doubling the diameter of its geographic range, a species would quadruple its RS. Therefore, to maintain constant density with a doubling of radius of geographic range, the species would have to quadruple its population size. Clearly this would require a high population growth rate if colonization were to proceed rapidly. Thus selection for high fecundity would be expected even among colonists inhabiting continents. Of course r- and K-selection are relative terms, and there are phylogenetic constraints on fecundity; hence, not all colonists are more fecund than all species from stable and saturated habitats. I suggest that since birds and small mammals are similar in several respects, including body size, endothermy, and those features of morphology and physiology common to amniotes, they are suitable groups for comparison.

Another generalization about colonists is that they are highly vagile. It thus comes as no surprise that birds are much more speciose on oceanic islands than are nonvolant mammals, since the latter are less likely to reach the islands. Furthermore, even within continents, bird species are generally found at more sites than are mammals.

Let us now return to the hypothetical species of mammal with the circular home range. Let us suppose that when still confined to a circle of 10 km radius, that the area in the outer circle yet to be colonized is a habitat mosaic. Furthermore, suppose that only part of this mosaic is suitable for inhabitation by the mammal species, the rest being to some extent or another, a barrier. If the patches of suitable habitat are large, colonization would be slow and patchy or might cease altogether. Thus for species that have low vagility, the extent of suitable habitat might be a poor predictor of RS. Furthermore, since species with a small RS have a higher overall extinction probability than species with a large RS, species that are poor colonists might be at greater risk of extinction.

Thus the evolution of a colonizing strategy should favor both relatively high fecundity and high vagility. However, nonvolant mammals are unable to acheive high vagility, even if they possess the high fecundity characteristic of a colonist syndrome. Small mammals of low vagility could reach high local densities as a result of fecundity or a lack of a dispersal sink to accommodate population recruitment. The consequence of a combination of high fecundity and low vagility would be species of low RS and high density. Of course selection could sometimes change this pattern. For example, restricted species of Peromyscus tend to be less fecund than more widespread species (Mace and Eisenberg 1982). Nevertheless, for nonvolant mammals in general, limits to vagility could preclude a positive correlation among RS, density and fecundity. In support of this assertion, for North American mammals, there is a nonsignificant and slightly negative tau-b correlation ($\underline{P}$ = 0.72, correlation coefficient = -0.017) between litter size and RS.

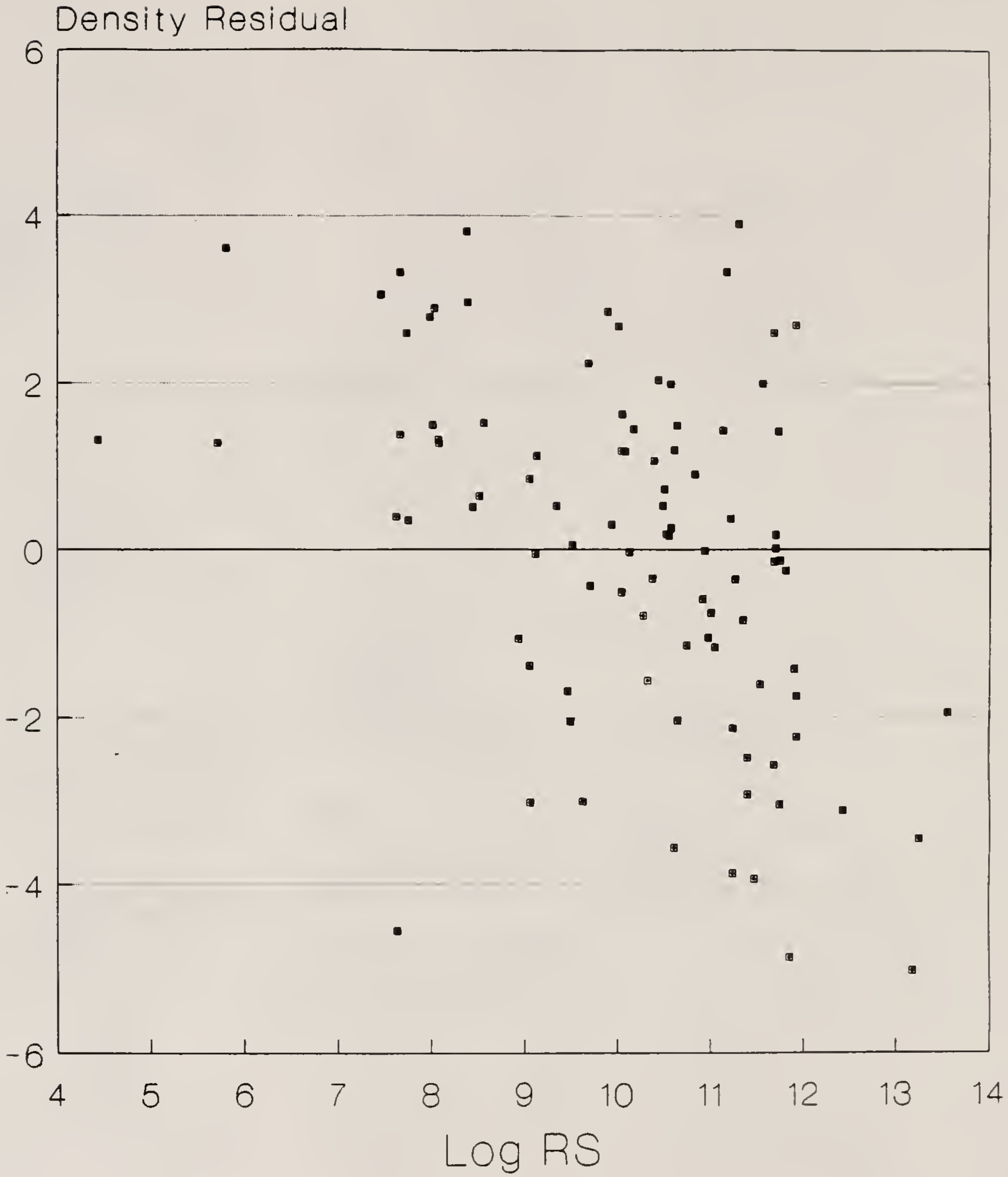
Low vagility also inhibits the rescue effect, whereby immigration counteracts loss of individuals from small, local populations. Comparative studies of birds and mammals as regards both primary colonization and the rescue effect include studies of nonequilibrium island biogeography and faunal surveys of oceanic and habitat islands. A general conclusion of such comparisons is that birds not only have higher initial colonization rates than mammals, but also a more pronounced rescue effect. The discrepancy in vagility of birds and small mammals is probably even greater in temperate climates, such as in the Nearctic, than in the tropics. It is easy to imagine a small species of bird colonizing a new habitat patch simply by slightly altering its annual migration. There is some empirical support for a generally greater dispersal ability in birds than in mammals. Using data reported in Rapoport (1982), I calculated a mean dispersal distance of 2.8 km/year for 14 species of mammals and 12.2 km/year for two species of passerine birds.

Thus birds, but not nonvolant mammals, can have both the fecundity and the vagility associated with a colonist syndrome. Similarly, for birds, but perhaps not for mammals, it may possible for a positive feedback to develop between RS and density. Although for both birds and mammals, high fecundity is likely to increase the number of propagules for potential colonization, an increase in RS is much more likely to result from this in birds than in mammals.

Furthermore, populations of small mammals trapped in small patches of habitat and thus thwarted from colonization would soon reach high population sizes, thus setting the stage for *K*- selection. In fact, populations that are unable to maintain a stable density in a small RS are likely to go extinct; hence, there might even be a species selection component to the negative association. If species in small RS are under stronger selection pressure to maintain stabler densities, then the RS/density association should be stronger in small RS. Fig. 1-2 supports this prediction. Fig. 1-2 is a scatter diagram of the residuals from an RS/density regression, plotted against the RS values for each density. Clearly RS and density are more tightly linked in species of small than in species of large RS. Furthermore, note that the data used in these analyses were logarithmically transformed; hence, plots of residuals of untransformed data show an even greater increase in scatter with increase in RS.

The notion that RS and density are more strongly correlated in species of small than in species of large RS

Figure 1-2. Scatter diagram of density residuals from a geographic range size/population density, linear regression, plotted against geographic range size values for each density. Data used in the analysis were naturally-logarithmically-transformed values for North American mammals.


Density Residual
6
4
2
0
-2
-4
-6
4
5
6
7
8
9
10
11
12
13
14
Log RS

is also consistent with the dichotomy between large and small mammals proposed by Caughley and Krebs (1983). They suggest that small species of mammals tend to have self-regulating populations, whereas the populations of larger species are extrinsically regulated. Since there is a correlation between RS and body size, we might infer that populations of species of small RS tend to be more intrinsically regulated that species of large RS. If small mammals were as vagile as large mammals, they might tend to be more extrinsically regulated. Although relevant data are sparse, I suggest that bats, which are among the most vagile of mammals, may prove to have more extrinsic regulation than small mammals in general. Not surprisingly, Nearctic bats tend to have large RS. Mammals, perhaps more than any other animals, seem to exhibit a tradeoff of traits characteristic of a good colonist. Small nonvolant mammals often have the high reproductive rate characteristic of good colonists, but are poor dispersers. Bats are good dispersers but have low reproductive rates. The endotherms that seem to be most successful at combining high reproductive rates and high vagility, are passerine birds, which also comprise the most speciose and widespread order of endotherms.

Birds might be more able than nonvolant mammals to circumvent the selection pressures within a restricted geographic range. Not only can birds more readily emigrate as densities become high, but the rescue effect will prevent populations in small patches of habitat from going extinct when population size is low. Furthermore, passerine birds in particular also have high reproductive rates; hence, their high species richness could be attributed at least in part to their ability to colonize habitat patches.

The process I have just posited to occur for mammals does not need to be strong to account for the slight negative density/RS correlation that remains in mammals after body size has been controlled. However, like the body-size-dependent species selection, it is a process likely to be more prevalent in mammals than in birds. In fact, mammals (exclusive of bats) are probably one of the few classes of animals that possess the dual combination of large range in body size, and low vagility, that are conducive to a strong negative RS/density correlation. Thus the apparently anomalous negative correlation might be caused by two fundamentally different but reinforcing processes. The more important of these processes is species selection that eliminates from the species pool those species that have small RS and a large body size.

The less powerful process is a decoupling of vagility from the general suite of characters associated with a colonizing syndrome. This decoupling need not be considered an adaptive trait but rather is simply a consequence of the greater constraints on vagility in nonvolant than in volant vertebrates. Alternatively, restriction to a small geographic range could impose K- selection on these populations, perhaps even leading to extinction of species of small RS that are unable to maintain dense populations. There is insufficient evidence to determine whether decoupling alone is responsible for the negative correlation, or whether subsequent natural and species selection should also be invoked. In any case, vagility should be considered when investigating the relationship between abundance and distribution of mammals.

Species Selection and RS

I interpret the results of the stepwise regression to be consistent with a model of species selection on RS. To reiterate and elaborate, energetics dictate the negative influence of HBL on density. Generally speaking, large species of endotherms require more energy than do small species. Hence, a given area will support fewer individuals, and therefore a lower density, of large than of small species. This effect of HBL on density is via natural selection, and the resulting negative correlation between density and HBL requires no species extinctions.

By contrast, the greater importance of density than of HBL as a predictor of RS is more readily explained by species selection. Neither density nor HBL should have a direct influence on RS, their effects occurring via their influence on population size. Species of large size should exist at lower densities (see above). Hence, for a given RS, large species should have smaller population sizes than small species. Note, however, that density and RS interact directly to determine population size, yet the relationship of HBL to RS could be primarily indirec. The purported sequence is as follows: HBL influences density, which interacts with RS to determine population size. Remember that in the species selection model of RS evolution, it is the extinction of species of small population size that results in a negative correlation between RS and density. Since body size is related to RS only indirectly, the correlation between HBL and RS is expected to be weaker than that between HBL and density. Thus species selection not only plays a role in the overall model of RS evolution, but it also provides a better explanation than natural selection of correlations among variables included in the model.

Finally, although it would have been preferable to conduct decisive tests among rival hypotheses, other hypotheses have not been proposed. I have seen no other speculations about the anomaly of the mammalian RS/density relationship; hence, I was forced to offer my own as starting points. As is often the case when exploring a new question, my conclusions were not definitive, but I hope I have compensated by making them thought-provoking and heuristic.

In the next chapter I will use RS and density to rank extinction probabilities of North American mammals.

CHAPTER II

A PRELIMINARY METHOD FOR RANKING EXTINCTION PROBABILITIES OF MAMMALS

Introduction

As noted by Thornback and Jenkins (1982), it would be wrong to assume that all threatened mammals are included in the official International Union for the Conservation of Nature and Natural Resources (IUCN) list because there are undoubtedly many taxa that are threatened but little known. Periods of great disturbance and mass extinction, such as the present, are expected to favor "*r*-selected" species over their relatives and Myers (1985) has pointed out that these species are in less danger of extinction. However, as I noted in the previous chapter, reproductive rate and colonizing ability have tended to become uncoupled in mammals, thus perhaps somewhat weakening the negative correlation between *r*-selected traits and extinction rate. Furthermore, there are some species that by typical mammalian standards would be considered *r*-strategists yet are still in danger of extinction, so clearly conservationists could make use of other methods to ascertain probability of extinction. Hence, many criteria have been suggested and used for various taxa and even general rules-of-thumb have been proposed. Unfortunately, although these methods are not necessarily mutually exclusive they are nevertheless often difficult to use comrehensively. For example, theory predicts that extinction probability correlates positively with both trophic level and body size. However, when one tries to apply these generalizations to predicting extinction probabilities of, for example, various species of the genus Microtus, the species are not readily separable. Since all Microtus are small herbivores, a prediction based on generalizations relating trophic levels and food habits to extinction, would be unlikely to indicate much difference among these species in probability of endangerment. It is, however, unlikely that all these species have identical or even very similar probabilities of extinction.

One approach to more precisely predicting extinction probability would be to attempt to take into account all the important variables that influence probability of extinction. Unfortunately the intensity of effort needed to acquire the relevant information for each species would be enormous, even if predictive models equal to the task were available. Alternatively, one could concentrate on one or a few especially predictive and readily quantifiable variables, and then use these variables to numerically rank all species by extinction probability. This method provides a practical yardstick of extinction probability, even for poorly-known species, by making use of existing endangerment information on other species. Therefore in this chapter I make more novel predictions about which species are likely to become extinct soon.

I herein suggest that population size is one of the most important criteria for assessing species endangerment. In a review of historic extinctions, Diamond (1984) noted that at every time scale examined, from a decade to evolutionary times, there is an inverse relation between extinction rates and population size, which is itself proportional to area and population density. Thus although small population size is not the only criterion for assessing endangerment, it is perhaps the most important, and is undoubtedly a factor considered by conservation agencies in determining endangerment status. Furthermore, population size can be estimated for many little-known species and then used as a guideline for determining allocation of further conservation effort. Since there may be species not currently designated as endangered but that have population sizes as small as those of species that are currently designated as endangered by conservation agencies, a ranking scheme could be used to troubleshoot for incipient endangerment. To this end, I attempted to compare population size estimates of endangered species with those of other species that have small geographic range size (RS) on the assumption that species with very small RS cannot have a large population size. Although this assumption is often wrong, the positive association between RS and population size is greatly strengthened when body size, trophic habits, and metabolic rate (i.e., endothermy vs. ectothermy) are controlled.

Realistically, I do not expect agencies to change any designations solely because of my estimates, but then this was not my primary goal in creating the estimates: my primary purpose was to pinpoint species of questionable status for further investigation. It is not practical to attempt an assessment of the conservation status of every species of North American mammal, so where does one begin? There are, for example, many species of mammals with a very small RS--are all these species at risk? In a world of finite resources, we should have a way to compile a short list of potentially endangered species from a much longer list of species with small RS, and then concentrate conservation efforts on species from the short list. Species that do not make the long list are probably at much less risk than species on the list and require no immediate action. By contrast, species on the short list should be investigated at once to determine their true endangerment status.

Species made my short list by having estimated population sizes within the same range as species currently designated as "Endangered" or "Vulnerable" by the IUCN in 1982. The officially designated species were thus used as benchmarks to assess the potential for other species to become threatened.

Of course this presupposes that there are always estimates of population size available, an invalid supposition. Therefore I sought methods to estimate population size. One such method is simply to make use of the purported positive relation between population size and RS. Generally speaking, species with larger RS have larger population sizes; and hence, are less prone to extinction. The problem with this generalization is that there is also much variation in population size that could be attributed to other variables, such as trophic habits, fragmentation of habitat, eurytopy of the species, and body size of the species. Unfortunately, using many other variables to make predictions of population size is often impractical (but see Humphrey 1985). Fortunately, there is one variable that correlates with several other variables and which can therefore act as a rough-and-ready substitute for them in an assessment of population size: that variable is population density. Indeed, since the population density of North American mammals varies over several orders of magnitude (Appendix C), any serious estimate of population size should account for density. I suggest that an estimate of population size that uses both RS and population density is superior to one that uses either variable alone even if one of the variables must be estimated indirectly. Furthermore, although such factors as habitat fragmentation and genetic variability also influence probability of extinction, these factors are difficult to incorporate with RS and density into a comprehensive, quantitative model. Thus I suggest that the best way to assess proneness to extinction is to first calculate population size, then to compare this estimate with values for known threatened species, then to modify this conclusion with other, sometimes qualitative information. In other words the calculations I present can be taken as starting points in the process of assessing endangerment status.

Thus I did not intend for this work to supplant that of specialists more familiar than I with the various taxa. My primary purpose was to act as a troubleshooter for the various specialist groups of the IUCN by screening lists of species for those with the potential of becoming threatened soon. The opinions of these specialists on my endangerment designations will fall into three categories: they will accept my designations, they will reject them or they will feel unqualified to either agree or disagree. If the specialists are confident enough to either agree or disagree with my designations, I will concede to their greater knowledge and consider the matter of the proper status of the species to be closed. If, however, the specialists are uncomfortable about either confirming or denying my assertions that certain species are endangered then those species should be investigated.

The IUCN apparently imposes no uniform techniques for determining population size (Thornback and Jenkins 1982), presumably for practical reasons. Most workers probably take into account both density and RS when making their assessments. However, probably few do so quantitatively by multiplying density times RS. The IUCN does provide a standard format, the Inventory Report Form, for reporting information on endangerment status; unfortunately much of the information they request is not available for most species (Thornback and Jenkins 1982). Therefore I proposed a method intended to be applicable to all nonvolant, terrestrial species of North American mammals. Although my method is likely to overestimate population size because it assumes the reported density obtains throughout the range of the species, it is often the only practical method. Furthermore, the population sizes of benchmark endangered species will also be overestimated by my method. Thus relative population sizes could be approximately correct even if absolute population sizes are in error.

Unfortunately even this crude technique often cannot be applied because either RS or density are frequently unavailable. For the particular biota I examined, Nearctic and Australian mammals, at least RS information is available for most species but density estimates were available for a much smaller number. This is not necessarily a fatal weakness, however, because density can be estimated indirectly from other parameters by taking advantage of interspecific relations between density and those parameters.

Materials and Methods

Unless stated otherwise, data for North American mammals were from Appendices A-D, and for Australian mammals from Appendices E and F. Sources of data for the appendices were listed in Chapter I. Variables for North American mammals included HBL, gestation length, litter size, a ranking of purported food abundance, population size, eurytopy, density, birth weight, length of lactation, growth rate, RS, genic polymorphism, genic heterozygosity and home range size. There were fewer variables in my data set for Australian mammals because the information was not available.

The analyses I used are described in Agresti and Agresti (1979), and computations were facilitated with programs in the SAS statistical package (SAS Institute 1985). First I assessed association of each variable with density using Kendall's tau-b, a nonparametric measure of association. I then used linear regression to establish quantitative relations for those associations that were found to be significant ($\underline{P} < 0.05$) by tau-b. Since density estimates were not available for many species, I used linear regression to predict densities based on information from species for which density is known. The final step was to compare the estimated population size against those calculated by the same method for endangered species. I used this method for Nearctic and Australian mammals. The two continents were analyzed separately. There were several reasons for not lumping the data for the two continents into a single assessment; one of these was that maximum possible values for Australian mammals cannot be as great as for the Nearctic, simply because the Nearctic is much larger than Australia. Another was that the interspecific patterns of relationship among variables might differ quantitatively between the two continents. Therefore the steps in my procedure will now be discussed in turn.

Assessing Associations Among Variables

Assessing associations among variables was useful for species of unknown density to screen variables of potential use as quantitative predictors of density. The procedure used for the screening, Kendall's tau-b correlation, does not provide quantitative predictions of values for one variable given a value for another variable. Nevertheless tau-b was useful in providing quick summaries of the strength and statistical significance of association of many variables. To test for association using untransformed data in correlation analyses from ANOVA or regression would have been misleading because many variables are not normally distributed. By contrast, the tau-b procedure uses ordinal scale information, does not require normally distributed data and will detect and measure any monotonic relationship.

Furthermore, tau-b, in contrast to Kendall's tau, can utilize ties. Hence, tau-b seemed the ideal measure for my purposes. Tau-b was also calculated for taxonomic levels below that of class, and the significant ($\underline{P} < 0.05$) correlations resulting from these are shown in Table 2-1.

Tests were conducted at the levels of genus, family, order and class, but only the significant correlations were listed and it was these that I considered suitable for further investigation. In fact, few of the regression analyses I subsequently performed were statistically significant unless the data were transformed, and the tau-b correlations were employed to indicate which variables would be most likely to have statistically significant linear regressions if they were transformed.

Calculation of Density

Usually direct density information was not available for a species of interest so I calculated density indirectly by making use of interspecific correlations of density with other variables. This method requires some explanation.

A rigorous scientist would probably consider it folly to predict the density of one species based on information from other species. Not only would the estimate probably be in error but there is no way to know how large that error

Table 2-1. Significant ($p < 0.05$) Kendall's tau-b correlations of density with other variables for North American and Australian mammals.

Variable	Taxon	P value	Correlation Coefficient
North America			
Eurytopy[a]	*Sciurus*	0.0374	-0.8889
HBL[b]	Leporidae	0.0487	-0.5714
Gestation Period[c]	Leporidae	0.0389	-0.7333
Gestation Period[c]	Insectivora	0.0415	-1.0000
Birth Weight[d]	Carnivora	0.0062	-0.5340
HBL[b]	Carnivora	0.0000	-0.8618
Litter Size	Carnivora	0.0142	0.4088
Gestation Period[c]	Rodentia	0.0019	-0.3298
HBL[b]	Mammalia	0.0001	-0.4536
Gestation Period[c]	Mammalia	0.0001	-0.5364
Litter Size	Mammalia	0.0037	0.2032
Food Abundance[e]	Mammalia	0.0005	-0.2658
Lactation Period[c]	Mammalia	0.0001	-0.3903
Birth Weight[d]	Mammalia	0.0000	-0.4146
Growth Rate[f]	Mammalia	0.0001	-0.4823
Home Range Size[g]	Mammalia	0.0001	-0.6631
Australia			
Litter Size	Mammalia	0.0390	0.3576
HBL[b]	Mammalia	0.0187	-0.3532

[a] Subjective ranking of habitat breadth. Ranking of 1 indicates extreme stenotopy, ranking of 4 indicates extreme eurytopy. Otherwise high values were reduced for species if they were highly localized within habitats.

[b] Head-and-body length in mm.

[c] Days.

[d] Grams.

[e] Subjective ranking of food abundance. Ranking of 1 indicates species is mainly a browser or grazer, ranking of 4 indicates species is primarily carnivorous upon vertebrates.

[f] Grams/day.

[g] Hectares.

is. Therefore scientific studies incorporating densities of several species have traditionally excluded species for which density data are not available. For detecting general interspecific patterns the deletion of a few points from a data set made up of many species is of no great moment but for someone working with endangered species the lack of density information for each species of interest could be crippling if densities are prerequisite to determining endangerment status. For species of unknown but possibly perilous status there is simply no time to wait for data from the field that may never arrive. I argue that in such a situation it is better to derive an indirect estimate than to let a species become extinct because we were never really sure it was threatened. Narrow confidence intervals and high certainty are difficult enough to achieve for common species, and for species in precarious survival status such assurance may be unobtainable. Our understanding of even the simplest natural systems is now barely within our grasp, yet now anthropogenic disturbances of wild populations have increased the complexity of natural systems to the point that our science has very little predictive power in many habitats. To expect conservationsists to achieve the same precision of prediction as conventional naturalists is unrealistic.

Another pragmatic reason for using indirect estimates is that there is almost no risk involved. One possible consequence of using my proposed method is that a species might be transferred into the 'endangered' category. If in fact the estimate is too low and the species is really not threatened, then the true status of the species would soon be discovered during rescue operations and further expenditure would cease. The American alligator (Alligator mississippiensis), for example, was once classified as endangered but is now subject to limited, controlled hunting. Conservationists would probably rather accept the embarrassment of an overestimated population size than the shame of having done too little, too late.

Another possible outcome of the indirect method is for a species to retain the designation of being not endangered, thus reaffirming the status conferred by conservation agencies. The species is then no worse off than if the estimate had not been undertaken.

The equations suggested for use in calculating density and their predictive abilities are summarized in Table 2-2. Printouts for the regression analyses from which the equations were made provided a variety of information including the significance level of the analysis, so I was able to eliminate from further consideration any nonsignificant ($P > 0.05$) relation from the list of predictive equations. Unfortunately, the least squares linear regression is only effective at detecting linear associations. In practice, the relations between variables using raw data were usually nonlinear and therefore nonsignificant even when I used variables that were found to be significantly associated by Kendall's tau-b. I therefore used transformations, which can linearize relations that are monotonic but superficially nonlinear. A variety of transformations was examined by trial and error, including exponentiation of the values for one or both variables. Some of the variable transformations that could be used for North American and Australian mammals are shown in Table 2-2 and can be calculated easily with a small computer or pocket calculator.

Even after excluding the nonsignificant relations from further consideration, there were often many possible significant relations at the level of class that could be used to predict density. The technique of multiple regression would seem to be ideal for estimating density from several other variables. Unfortunately, as pointed out in Chapter I, this technique excludes observations that have missing values for variables. Since data for more than two or three variables was unavailable for most species, the resulting multiple regression equation would rely on a very small sample size and would not provide even approximately reliable estimates.

Therefore I deemed it most appropriate to use only one variable. However, for the reader more interested in making accurate estimates of population size than in ranking

Table 2-2. Regression equations used to estimate density of North American and Australian mammals.

Variables	R^2	Intercept	Slope
North America: Mammalia			
Log Density, HBL$^{.50}$	0.480	5.0130	-0.2670
Log Density, Log Gestation Period	0.531	11.9818	-3.1189
Log Density, Log Litter Size	0.080	-2.2091	1.8796
Log Density, Log Lactation Period	0.351	11.1570	-3.0405
Log Density, Log Birth Weight	0.405	2.0715	-0.8556
Log Density, Log Growth Rate	0.434	1.7706	-1.0997
Log Density, Log Home Range Size	0.778	1.3292	-0.7337
North America: Leporidae			
Log Density, HBL	0.552	5.6649	0.5222
Log Density, Log Gestation Period	0.718	62.3078	-16.6110
North America: Carnivora			
Density$^{.25}$, Birth Weight$^{.25}$	0.552	0.6409	-0.0946
Density$^{.25}$, HBL$^{.25}$	0.437	1.0126	-0.1268
Log Density, Log Litter Size	0.039	-6.1365	1.7378
Log Density, Log			
North America: Rodentia			
Gestation Period	0.463	10.4537	-2.5078
Australia: Mammalia			
Log Density, Log Litter Size	0.290	-0.9821	1.2859
Density$^{.333}$, Log HBL	0.316	3.3780	-0.3906

[a] Natural logarithm.

extinction probability, I have also listed some associations for several variables and at several taxonomic levels.

The choice of which variable to use for a predictor was somewhat subjective. One might be inclined, as I was at first, to invariably choose the variable exhibiting the strongest association with density. There are, however, reasons why this is sometimes inadvisable. First, the strength of association for each variable varied unpredictably with taxonomic level. Thus the variable exhibiting the strongest association at one level did not necessarily yield the strongest association at another. Although I could have chosen for each species the regression providing the highest coefficient of determination, the estimates would not be comparable between species if different equations were used for each species. I reasoned that a single equation that could be used for all species would be more useful in ranking extinction probability than would equations useful for a taxonomic subset of the species--even if the R^2 for regressions using certain taxa were higher than the one for the class as a whole. Thus to solve the first problem I chose the taxonomic level of class, since only associations at this level would be applicable to the entire data set.

Secondly, data were often unavailable for many variables for many species; hence, a strong interspecific correlation between variables was useless when the information for one of the variables was lacking for the species of interest. Furthermore, subsequent analyses revealed that estimates of density varied considerably depending on which variable was used to estimate them. To solve the second problem I had to concentrate on variables for which information was available for the most species. Those variables were RS and HBL. As explained below, RS was not suitable as a predictor of density because RS is also used in the equation RS times density equals population size. HBL, however, was available for almost every species, and was therefore the variable chosen to estimate density. For general interest I have also listed other equations that could be used to estimate density, but will not discuss them further here. The equation used to calculate densities of North American mammals was $\text{Log Density} = -0.2699\ \text{HBL}^{.5} + 5.01300$. The equation used to estimate densities of Australian mammals was $\text{Density}^{.333} = -0.3906\ \text{Log HBL} + 3.37802$. For the interest of specialists, the details used in calculating density and population size by using SAS are elaborated in Appendix G.

Better-fitting first-order equations than any I listed might exist, since it is possible mathematically to derive an exact polynomial equation for the relationship between the variables, based on the data included in the calculations. Unfortunately such an equation would be very complex and would be unrealistic unless new data fell exactly along the curves calculated to link the existing data points (Agresti and Agresti 1979). In other words, an equation fitting the data points exactly would be indicative of a completely deterministic association, which is unrealistic. Furthermore, more complex models are not parsimonious and are usually not preferred unless they are supported by other information.

A major difference between the Nearctic and Australian sets of analyses was that there were many more density estimates available in the literature for the Nearctic than for the Australian mammals; hence, the predictions for the former are probably more accurate. Note also that bats (Chiroptera) were excluded from both data sets; and hence, my predictive equations are not appropriate for the Chiroptera. The genus *Peromyscus* was also excluded from the North American analyses for theoretical reasons, to assure independence of another part of my study from one by another author. Nevertheless the interested reader could use methods similar to my own to calculate population sizes for species in that genus.

Calculation of Population Size

Once densities were available they were multiplied by RS to estimate total population size for a species. When recent numerical estimates of RS were not available from the literature I calculated RS from current distribution maps by using a planimeter. Of the nonvolant, terrestrial species of

North American mammals considered to be endangered by the IUCN and compiled by Thornback and Jenkins (1982), most are technically only subspecies. Several of these are, however, full-fledged species. It was these that I used as my benchmark species, although the technique could probably be modified to include subspecies. Note that the RS figures that I used for this study were not the same as those I used in other studies for the same species in other chapters. The other chapters are concerned with evolutionary ecology and assume RS to be an evolved characteristic; for such investigations it is probably better to use values for RS that more nearly reflect Precolumbian selection pressures. By contrast, the current study is concerned with anthropogenic extinction and does not assume that the RS of species have had sufficient opportunity to reach a new ecological equilibrium.

For the current study I was most interested in establishing the maximum population sizes that are associated with threat of extinction on the grounds that species with population sizes as small or smaller than these are also threatened. That is, to establish population size guidelines for endangerment it is not the smallest RS associated with threat that is of interest, but rather the largest RS. Using RS values from populations so small that the species is virtually extinct would greatly underestimate the minimum RS necessary to curtail extinction, so I endeavored to do just the opposite: that is, to use the maximum RS associated with a high probability of extinction. For both theoretical and practical reasons I was not able to determine exact maximum RS sufficient to remove immediate threat of extinction, but my estimates are as objective and fair as was possible for me to make. Thus the values for RS used as benchmarks were not necessarily the most recent estimates for the species in question; my rationale for sometimes using older RS values was that species sometimes become endangered before they reach their current, very small RS.

By now the reader may have guessed one of my reasons for excluding RS from the correlation analyses: RS varies over evolutionary time to a degree that is important to conservationists. Furthermore, in the equation, (population size = RS multiplied by density), the factors would not be independent if the density estimates were calculated by the method discussed above. This is because the method uses other variables to calculate density; hence, if RS were used to estimate density then the population size estimate would really be calculated by multiplying RS times a correlate of RS. Thus to avoid circularity, RS was not used to calculate density estimates that were used in the estimation of population size. The loss of RS as a predictor of density is not, however, critical, because there are other variables that are just as useful as predictors. Thus, by maintaining

RS as a variable completely independent of density it was possible to calculate how changes in RS affect population size.

It should be emphasized that the estimation technique I propose is only as good as the data used in the analyses, but the actual model is iterative and subject to improvement with new information, such as changes in RS. One process in particular, habitat fragmentation, is likely to result in many overestimates of population size (eg., Harris 1984) unless a correction is employed that reflects the total loss of RS resulting from fragmentation. Habitat specificity should also be considered at the same time, if possible.

Results

Estimated population sizes for the least abundant species are shown in Tables 2-3 and 2-4. The values ranged widely and the population sizes of threatened species overlapped considerably with those of the other species. I have excluded many species of very low population size from the lists, especially the Australian list. The species excluded are well-recognized in the literature as being scarce so inclusion in my list would be redundant. Furthermore, the purpose of my list was not to name every species of low population size, but to highlight species whose status is unknown and perhaps precarious, for further study.

Table 2-3. Estimated abundances for selected species of North American mammals.

Species	Abundance
Bison bison	48,735
Cervus elaphus	1,551,301
Cynomys parvidens[a]	5,069,654
Dipodomys elator[a]	1,262,389
Eutamias ochrogenys	4,910,734
Eutamias palmeri	1,416,971
Marmota olympus	140,014
Oreamnos americana	1,157,690
Ovibos moschatus	121,520
Ovis canadensis	4,494,371
Ovis dalli	1,362,432
Rangifer tarandus	4,032,024
Reithrodontomys raviventris[a]	4,123,971
Sorex alaskanus	130,219
Spermophilus mohavensis	3,127,124
Spermophilus washingtoni	2,161,235
Thomomys bursarius	1,634,006

[a] Classified as endangered or threatened by the IUCN.

Table 2-4. Estimated abundances for selected species of Australian mammals.

Species	Abundance
Antechinus godmani	2,436,178
Antechinus leo	4,961,616
Echymipera rufescens	1,995,144
Hemibelideus lemuroides	2,123,998
Hypsiprymnodon moschatus	3,013,174
Macropus bernardus	911,015
Macropus irma	3,476,967
Macropus parma	2,691,405
Melomys cervinipes	4,648,724
Perameles gunni	4,640,024
Petrogale burbidgei	2,179,339
Potorous longipes	1,722,284
Pseudocheirus herbertensis	2,001,286
Pseudomys pilligaensis	3,871,735

The Australian species presented an unexpected problem. Many species of Australian mammals have estimated population sizes below those I estimated for endangered species. Since my purpose was to come up with a short list of species in need of further study, I needed some way to pare this number down. By consulting the literature I discovered that several of the species on my list were apparently extinct. Although a more assiduous study of the literature would have excluded these species from initial consideration, their very inclusion on my short list suggests that my method is useful as a predictor of extinction probability. In any case, the list presented is one from which extinct species, as well as extant species whose conservation status is already well-known, have been excluded.

Note that the lists can be lengthened simply by inclusion of species with slightly higher estimated population sizes. Those so inclined need only to use the data from the Appendices and the equations presented herein to estimate the population sizes of other species of North American and Australian mammals. I somewhat arbitrarily chose as a cutoff point for Nearctic mammals, the population size of the most populous of the endangered species of North American mammals. However, interested investigators could use a value of their own choosing.

Discussion

An estimated population size within range of known endangered species is cause for alarm. The status of these species warrant investigation. The estimated values for population size should not, however, be taken as reliable. One should especially avoid comparing population sizes of Australian and Nearctic mammals, because the two sets of estimates were calculated from different equations. Furthermore, specialists could easily criticize the values for certain species. For example, my equation estimates population size of the river otter (*Lutra canadensis*) to be over fifteen million, which is almost certainly an overestimate. Thus there is no substitute for basic natural history information, and my estimates should be considered as rough guesses of greatest utility when relevant natural history information is lacking. For many species, we have little more to go on than measurements from museum specimens, and a map of the geographic range. For these species, my equations, imperfect though they may be, are a first step in ranking extinction probability.

CHAPTER III

A SHOTGUN MODEL OF ADAPTIVE RADIATION AND EXTINCTION

Introduction

The previous chapter used natural history information to predict extinctions. In this chapter I take a much larger view of the extinction process in nature. In the three subsequent chapters I will explicate this model and test hypotheses derived from it.

Let us first consider the level at which selection occurs. The rate of natural selection is probably highest at the level of the individual and some authors have defined natural selection to occur only only among individuals of a population. Species, however, do not all survive and produce new species at the same rates. When there is a pattern to this differential survival then a type of selection could be said to occur at the level of species. This concept of species selection has been presented under several different guises. Grant (1989) prefers the term "speciational trends" and describes the venerable history of the concept. One of the more popular discussions of species selection is found in Stanley (1979), but perhaps the least controversial description of the basic principles is Fowler and MacMahon (1982). Briefly, if the species that survive longest and/or speciate most rapidly exhibit characteristics that differ from those that do not, then the overall character of the biota will shift.

There is much discussion in the literature concerning the ecosystem importance of extinction of species. For example, the extinction of most species of large herbivorous mammals during the Quaternary of North America not only resulted in a statistical decrease in the body size of herbivores, but also deleted their predators and scavengers from the vertebrate roster and probably increased the abundance of small herbivores (Webb 1969, 1984). The extinctions in South America were even more profound. In the Pleistocene there were as many genera of large (>44 kg) mammals in South America as in any of the other continents, including Africa (Martin 1984). During the Pleistocene, however, extinction of megafauna was extensive in the neotropics, so that today Africa has far more genera of large mammals than South America. Since megafauna exert different ecosystem effects than microfauna (e.g., Caughley and Krebs 1983; Emmons and Gentry 1983; Kortlandt 1984; Cristoffer 1987) it follows that these extinctions held some ecosystem importance.

Pushed to its logical extreme every extinction or speciation event will shift the overall character of the biota to some extent because every species has some unique characteristic, and obviously the extinction of species that are hosts in obligate ecological relationships will result in the subsequent extinction of their dependent species. Normally, however, the loss or addition of a small number of species is not expected to markedly affect the "gestalt" of the community unless the species are unusually important (i.e., if they are keystone species). However, the loss or addition of many species over a short interval of time often has profound effects, especially if the species lost are a nonrandom subset of the total biota (e.g., Stanley 1979; Fowler and McMahon 1982; Webb 1969, 1984). Furthermore, extinctions over longer intervals could also produce trends, although these may be more difficult to detect. I will hereafter refer to the selective processes that occur above the taxonomic level of species as "higher-level selection." I also suggest herein that brief but massive pulses of extinction, such as those engendered by humans, leave a different signature on the evolutionary record than do background levels of extinction.

Thus I assumed that selection could occur at any taxonomic level. However, there are theoretical reasons for believing that selection is more prevalent at some levels than at others. Selection might occur at levels of organization below that of individual (e.g., Dawkins 1976) but if so is beyond the scope of this work. Restricting myself to individuals or more inclusive entities, I considered that a prerequisite for selection is discreteness of the units selected. For example, if one accepts for a definition of evolution one used by population geneticists, "a change in allele frequencies among generations" (Endler 1986) then the removal of clones from a population of plants or cells from a metazoan is not natural selection because the genotypes of the individual units removed are continuous with those that persist and thus allele frequencies remain constant. Individual mammals are, however, discrete entities; hence, selection may be common among them. Species are also relatively discrete, albeit somewhat less so than individuals when hybridization occurs. Taxonomic units above the level of species are even more genetically discrete than are species. There are, however, levels between that of species and individual in which the units are often too indistinct to meet the prerequisite for selection; among these are kin groups, social groups, demes, populations and subspecies. Therefore I will not discuss selection at these levels.

If higher-level selection occurs it must be at a much slower tempo than that of natural selection because there is a greater turnover rate of individuals than of species. Higher-level selection might thus be observed as a long-term trend. During the span of the few months or years available for a typical scientific investigation there are too few extinctions and speciations for trends in extinction and speciation to be detected, but the geological record might reveal them. Rensch (1960); Webb (1983, 1984) Knoll et al. (1984) and Vermeij (1987), among others, have described many such trends, and Kurten (1971), in a capsule summary of evolutionary trends among mammals in the Tertiary, even remarks of a general increase in efficiency, beauty, gracefulness and elegance. More prosaically, trends at lower taxonomic levels are often implicit in discussions of evolutionary polarity, and transitions from primitive to derived can be interpreted as trends if they occur in several sequential steps. Long-term trends are sometimes better explained by higher-level selection in conjunction with natural selection, rather than by natural selection alone. Speciation and the extinction of species have been proposed to sometimes work as a ratchet, permitting directional changes of a magnitude not possible for natural selection. A recent example of this concept is provided by the equids, the evolutionary record of which is fairly well known. Earlier interpretations of horse evolution depicted an unbroken lineage of taxa with progressive characteristics, such as increasing hypsodonty, size, and relative limb length. As the record became more complete it became apparent that this interpretation was an oversimplification (McFadden 1985). Although general trends did occur they were confounded by radiations which sometimes obscured the overall directionality of the process. Someone observing only extant equids would be unlikely to detect overall trends because there would not have been enough time for selective extinction and speciation to occur.

The characteristics of individuals within a species are not, however, determined by higher-level selection; they are determined by natural selection at lower levels, especially that of the individual. When there is a loss of individuals from a population, there is potential for invoking natural selection; all that is required is that the individuals lost differ significantly in value for heritable traits from those individuals that persist; and that both are from "equivalent" environments.

Similarly, for higher-level selection to be important the species lost must have heritable traits that differ from those of individuals that survive. In a given biota both processes can and probably do occur, but usually only natural selection occurs sufficiently rapidly for study by mankind. The problem then becomes one of detecting the effects of higher-level processes from the background level of selection among individuals.

The Basic Model

Adaptive radiation has also been called explosive radiation, a term that suggests species burst into being as a riot of adaptive types. An elaboration of this concept is herein suggested as a useful heuristic tool.

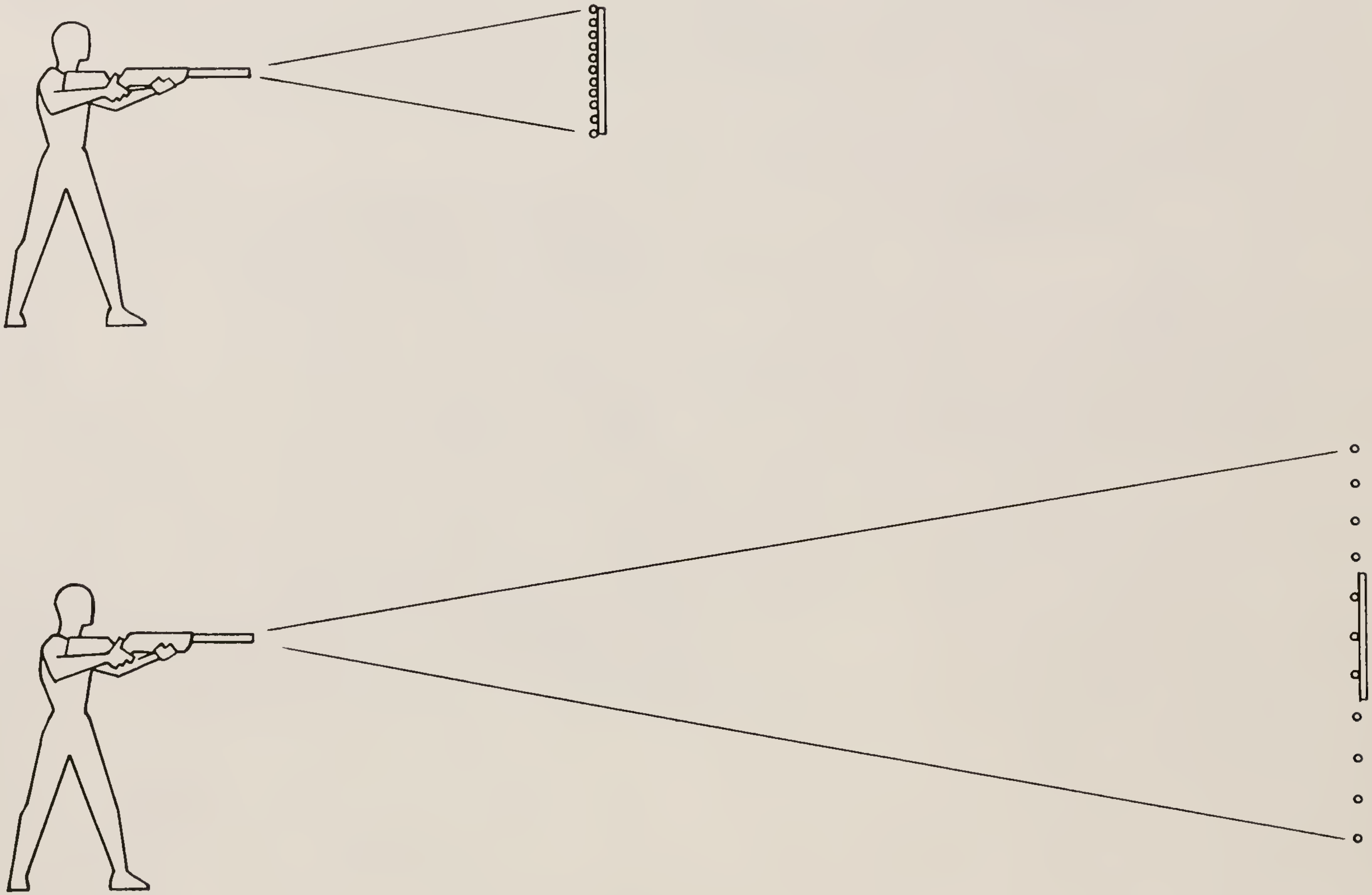
Imagine viewing a slow-motion film of a marksman firing a shotgun at a target. When the shotgun pellets leave the gun they are close together and all seem to be heading in approximately the same direction. However, as the pellets approach the target they will begin to diverge, and if one could film these in extreme slow motion it would then become apparent which pellets have the most divergent trajectories. Eventually the pellets will travel as far as the target, but if the target is small and distant only a few pellets will strike it; the rest will miss because of their divergent trajectories (Fig. 3-1).

Now, after shooting is finished it is quite easy to see which pellets were on the correct trajectory to hit the target because they will be imbedded in the target. Note, however, that at the instant the shot was fired there was no practical way to determine which pellet would strike the target. The marksman must wait until the shooting is over in order to determine his hits and misses, and even a technician using sophisticated high-speed cameras would have difficulty predicting which pellets would strike the target when the pellets were only an inch from the barrel of the gun.

Pursuing this analogy further, if explosive radiation can be likened to the firing of a shotgun then we can also consider the marksman to be the ancestral species and the target to be long-term survival of species. In reality,

Figure 3-1. Species selection can be analogized to a shotgun blast. In this figure time is represented by distance, adaptive radiation is represented by a shotgun blast and survival is represented by the target. Note that long periods of time are necessary to determine which species survive.

Extinctions Produce Patterns



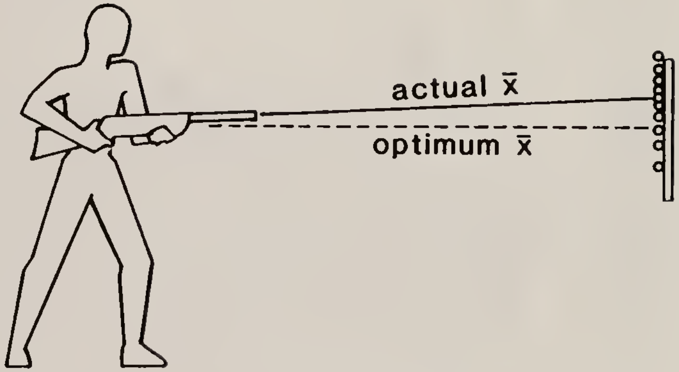
gravity alters the trajectory and therefore the distance pellets will reach, but for the purpose of this analogy let us assume the gun is fired in the absence of gravity.

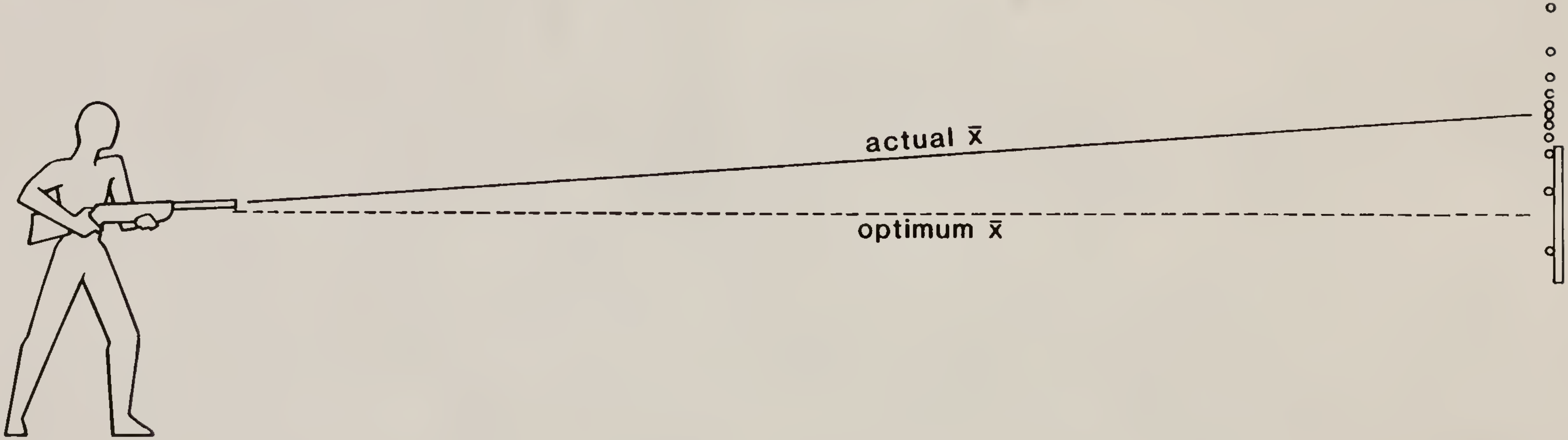
To continue with the analogy, note that if the target is large and close to the marksman then all the pellets will strike the target. Similarly if we observe an adaptive radiation immediately after it occurs a high proportion of species will be seen to survive. But if the target (survival) is moved farther away fewer pellets (species) will strike it (Fig. 3-2). The farther away the target, the longer it will take the species to reach it and the more important deviation from the optimum trajectory will become in determining long-term survival. I will now digress for a moment to discuss what "survivors" really are.

In reality all species are both survivors and failures because all species survive for some length of time, yet all will probably perish eventually. The comparison intended herein is between those species that are relatively long-lived and those that are shorter-lived. Thus the terms "survivors" and "failures" are actually shorthand for "species of large actual stratigraphic range" and "species of small actual stratigraphic range".

Continuing with the shotgun analogy, it can be seen that the easiest way to determine which species have the optimum trajectory for survival is to wait until the shoot

Figure 3-2. A special feature of the shotgun model depicted in Fig. 3-1. Note that long periods of time are necessary to determine the characteristics of long-lived species.


actual $\bar{x}$
optimum $\bar{x}$


actual $\bar{x}$
optimum $\bar{x}$

is over and study the survivors imbedded in the target. The radiation itself may be interesting but radiation at its peak tells us nothing about large scale trends in evolution. Only by studying the aftermaths of several firings can we generalize whether the marksman tends to bias his aim in a certain direction; similarly, by examining the aftermath of several adaptive radiations we might detect a trend in extinctions.

To elaborate, if the marksman's aim is a bit off, only the pellets near one edge of the scatter will strike the target. Thus the mean trajectory of the pellets as they leave the gun could well differ from the trajectories that belong to pellets that strike the target, in which case the mean trajectory of the pellets as they leave the gun would not be the optimum trajectory to strike the target. Similarly the general trends apparent during an adaptive radiation might not be the ones consistent with long-term survival. Note also that the farther away the target is from the marksman, the easier it is to tell if he is a bad shot, and the longer we wait after an adaptive radiation the easier it is to tell whether short-term trends differ from long-term trends. The longer the time elapsed after radiation the more species are likely to become extinct and the more selective extinctions and speciations have occurred.

This principle can be illustrated at a higher taxonomic level by an example from the Miocene epoch of North America, as discussed by Webb (1983). At the beginning of the adaptive radiation of savanna ungulates in the Miocene of central North America, there were a moderate number of genera of browsers but few or no grazers. Then, coincident with climatic changes, the vegetation took on a more open aspect as savanna woodland and grassland replaced closed-canopy forest. As grassland interdigitated with forest a variety of grazers and mixed feeders evolved, such that at the peak of diversity in vegetative structure, a rich fauna of browsers, grazers, and mixed feeders was present. However, as the climatic trend toward coolness and aridity continued, forest-dwelling mammals began to disappear altogether on the Great Plains and browsers became extinct at a faster rate than they evolved. Eventually the species richness of grazers declined as well, with the ultimate result of the climatic trends being the impoverished ungulate fauna of the Great Plains of present day North America. Note that a biologist living at the peak of species richness would probably not be able to predict which morphologies and food habits would persist the longest after the radiation. With the advantage of hindsight made possible by a good fossil record we can discern the loss of evolutionary trajectories inconsistent with long-term survival. Thus even though Webb (1983) did not address intrageneric extinctions the process described therein is consistent with my own model in at least one important aspect: the taxa that survived were a very nonrandom ecological subset of the original adaptive radiation. Clearly in both my study and that of Webb, there were selective agents at work weeding out species unsuited to changing conditions. It would be inappropriate to attribute the trend to natural selection alone, because few or none of the identified changes in character state were intraspecific (unless you consider the changes that occur at speciation to be intraspecific). It was the community as a whole that changed, by adding and deleting species with certain character states. The point I have tried to make with this example is that evolutionary changes are sometimes so subtle and so slow that they can only be detected by observing through a very wide window of time, and certainly are not easily discerned in the midst of an adaptive radiation.

There are many other examples illustrating that the survivors of adaptive radiations are usually specialized subsets of the taxon. For example, the longest lasting forms of ammonite molluscs shared a morphological structure that is thought to have enabled them to live at great depths (Ward and Signor 1983). Another example is that of Paleozoic hydrozoans (marine invertebrates), in which the morphologically complex genera had the greatest longevity, at least during the intervals between mass extinctions

(Anstey 1978). There are many such sequences of radiation, extinction, and reradiation of the survivors among South American marsupials and other mammals (Simpson 1961; Pascual *et al*. 1985), and perhaps in other faunas as well. As a final example, among benthic molluscs and some other invertebrates the mode of larval development appears to have had an important influence on extinction rates. Locally-extirpated populations of the species with more sedentary larvae are often unable to recolonize after extirpation, but more pelagic larvae can do so. The more sedentary species are probably better competitors under stable conditions but fare poorly during periods of great disturbance. Periods of great environmental disturbance can be analogized to a mass extinction event, albeit on a local scale (Hansen 1980; Jablonski and Lutz 1983).

Thus, periods of great environmental change tend to favor generalized species (Jablonski 1986), as predicted by *r*- and *K*-selection theory. Someone observing a biota under flux might conclude that long-term trends would favor the generalized species to be seen prospering during a perturbation. However, biotic succession exemplifies the concept that a change in conditions could reinstate long-term processes that favor other species than those that prosper during disturbance. I suggest that the relative importance of natural vs. species- and higher-level selection changes with time elapsed since the most recent adaptive radiation. Furthermore, there are long-term evolutionary trends (e.g., Vermeij 1987); mosaic evolution occurs, especially in vascular plants (Knoll *et al*. 1984); and kin and sexual selection have enhanced the evolutionary success of many organisms (e.g., eusocial species) in ways that could not have been predicted by natural selection theory until it was greatly modified, a problem of much concern to Darwin. However, perhaps the most interesting challenge to the traditional concept of evolution by natural selection is the amount of control that some organisms seem to have over their genetic destiny. This is exemplified most completely by structurally dynamic genes, as summarized in Campbell (1982). There are, for example, dynamic genes that sense their environment and change structure in response to detected conditions; automodulating genes that change their future responsiveness to stimuli when stimulated; and experiential genes that transmit specific modifications induced in somatic phenotype to descendants. There are as yet no examples identified of genes that acquire changes in anticipation of their usefulness, although of course genetic engineering enables humans to do so. All of these phenomena attest to the notion that some understanding of natural selection alone is far from being synonomous with a comprehensive knowledge of organic evolution, a sentiment recently reiterated by Endler and McLellan (1988).

Furthermore, although my investigation is primarily concerned with certain aspects of macroevolution, this does not require that we abandon all hope of finding general principles of selection that apply to any taxonomic level. For example, a possible parallel of higher-level selection discernible among individual-level variables is that of the logistic growth curve. A population in an exponential growth phase is likely to be under different selection pressures than when it is close to the carrying capacity of the environment, and if one form of selection predominates long enough, it is likely to result in a character shift in the population as a whole.

Jumping to the level of species, we can see a similar process at work. Pimm *et al*. (1988) have shown that the attributes rendering species most sensitive to extinction shift with population size; perhaps they also shift with time. An adaptively-radiating clade corresponds to *r* selection at the species level, whereas a very old monospecific genus could be nearer the *K* end of the spectrum. Just as *K*-strategy species tend to have greater longevity than their close relatives that are *r*-strategists, species that survive adaptive radiations could differ from those that perish. Besides longevity, surviving species might be predicted to have other characteristics of *K*-strategists, including greater body size, longer gestation and lactation periods, higher birth weights, larger home and geographic range sizes, and lower densities. Dial and Marzluff (1988) suggested that during periods of large fluctuation of environmental conditions, species of small body size are favored, whereas during periods of stability, large sizes are favored. This is consistent with my own model in which small size predominates during exponential (radiating) phases, but large size is selected for at equilibrium. Furthermore, Dial and Marzluff have also studied life history traits of taxa that affect extinction and speciation, but their work had not gone to press at the time of this writing.

A logistic model for diversity of orders of marine metazoans was elaborated and tested by Sepkoski (1978, 1979, 1981) and I suggest that the same is true for Cenozoic land mammals. I have already suggested as a general principle that species in the midst of adaptive radiation will tend to differ in predictable ways from species that are not. Thus in some small way I have wedded the process of exponential adaptive radiation proposed by Sepkoski to evolutionary trends, such as escalation, a process proposed and dicussed at great length by Vermeij (1987), Dial and Marzluff (1988) and others. I now advance a more precarious prediction, namely that evolutionary escalation is a major cause of the collapse of an adaptative radiation. Thus I hypothesize that the improvements associated with escalation will be measurably more pronounced in species that persist the longest during periods of adaptive radiation, or that survive past the radiation altogether. I did not test this hypothesis and only offer it as food for thought.

Shotgun Blasts and Logistic Growth--a Unification.

In summary, I suggest that adaptive radiation is analogous both to the blast of a shotgun and to the logistic curve. Species come into being as variations on a theme occurring in a single genus. These variations are constrained by laws of development and design and can be arrayed in a systematic fashion manifested by correlated trends among variables.

Extinction then occurs within the genera, the long-term survivors of which will differ from more ephemeral species in the same ways that *r*- and *K*- strategists differ. Higher-level selection could also occur over short intervals of time, as during mass extinctions. However, such selection is difficult to separate from natural selection. By contrast, long-term trends are largely attributable to species- and higher-level selection; hence, the most unequivocal examples of species- and higher-level selection come from long-term trends, not from periods of mass extinction. In the next three chapters I will explore macroevolution in mammals and attempt to discern long-term trends by comparing patterns among variables that arose over a short time span with patterns that arose more quickly or more recently.

CHAPTER IV

PREREQUISITES FOR THE SHOTGUN MODEL

Introduction

In the previous chapter I speculated that adaptive radiation produces speciose genera of many short-lived species. Although the protracted nature of species selection renders impractical the direct observations necessary for its evaluation, in the next chapter I will test hypotheses relevant to making inferences about the importance of this process. First, however, I wanted to establish whether prerequisites for the shotgun model are met. If the prerequisites necessary for the process to occur do not exist then I would be premature to invoke the model to explain patterns I discern from the results of analyses.

One condition certain to be met for extensive species selection within genera is that of heritability. Both natural and species selection assume that in the absence of mutation, genotypes of offspring are derived from their parents. This assumption has been confirmed numerous times and is the cornerstone of the science of genetics.

The second major assumption of a model that incorporates extensive intrageneric selection, is that there is considerable variation among species for selective agents to act upon. In the simplest case, that is when there is no variation in values for traits, then there is no possibility for selection. Furthermore, it is intuitive that the rate of selection is likely to be greater when the variation is large than when it is small, because large differences should be more readily discriminated by selective agents than will small differences. However, even when one allele is clearly optimal for a given population at a certain place and time, the members of populations often do not coverge on this optimum even after many generations. Reasons for lack of fixation include gene flow, mutation, changes in the environment that alter selective pressures, and recombination, which will be discussed shortly. Intrageneric species selection might, however, more frequently result in optimal genotypes than will natural selection. The reason for this is as follows.

Recombination among members of a species mixes optimal and suboptimal alleles, whereas recombination does not occur among species in a genus (unless they hybridize). Thus, a large amount of variation within a species might not necessarily enhance selection because much of it is masked by dominant or codominant alleles. Since selection acts on the phenotype, it is quite possible and frequently occurs that deleterious alleles persist for many generations as recessives. By contrast, since there is no recombination among species, distinctions among them are probably more apparent to selective agents than are many differences among individuals in populations. Lack of recombination at higher taxonomic levels probably also tends to make selection more permanent than within populations. This notion is not new and has been elaborated by some workers (e.g., Fowler and MacMahon 1982) to explain the predominance of sexual over asexual reproduction in nature. Briefly, the genetic variation sexual species maintain by recombination and dominance, serves to hedge bets against changes in selection pressures. Asexual species, which cannot create new gene combinations by recombination, suffer a higher extinction rate than sexual species. Note that there is no mechanism to allow the persistence of a species of low population size analogous to the one that maintains recessive alleles in a population. In a sense, then, the much greater species richness of sexual than of asexual species can be attributed to a form of reproduction that partially thwarts extinction and species selection.

Nevertheless, the purported weaker correlation between variation and rate of selection within populations should not blind us to the likelihood that variation correlates strongly with extinction rate among species or higher categories. A positive correlation between amount of variation and rate of species selection is intuitive and will be assumed in this chapter. An extension of this assumption can also be applied to the various taxonomic levels. Taxonomic levels with large variances for characters should be especially prone to species selection. Thus we might consider a taxonomic level with high variance for several characters to be a good place to look for the effects of species selection. Although I believe this assertion to be generally valid, it is also an oversimplification.

One complication is that lower taxa are nested within higher taxa; hence, variance at one level is not independent of variance at another level. Fortunately there is a procedure, the nested analysis of variance, to measure the variation within levels of a nested hierarchy while controlling for other levels. I included the levels infraclass or superorder (i.e., monotremes, marsupials and placentals), order, family, genus and species in my nested analyses of variance on North American and Australian mammals. I followed Strahan (1983) in recognizing two orders of marsupials, the Polyprotodonta and Diprotodonta. The variables I analyzed for both continents were HBL, RS, length of lactation and litter size. Additionally, for North American mammals I included stratigraphic ranges of fossil species that lived at some time during the interval from the Hemphillian (Miocene) to the Recent. These data are from Appendix 2 of Kurten and Anderson (1980).

The reader should be aware of certain subtleties in the interpretation of the nested analysis of variance. The variance at each taxonomic level is a measure of the amount of variation that can be attributed to differences among, not within, the units at that level. This can be illustrated with a hypothetical example.

Suppose a nested analysis of variance, similar to the ones I used, was performed on a data set containing body size information (logarithmically transformed) on living species of Nearctic mammals of the orders Insectivora and Artiodactyla. The former order contains shrews and moles, whereas ungulates comprise the latter. Thus there would be no overlap in size among the two orders and a nested analysis of variance would indicate that almost 100% of the variation in body size occurred at the level of order. This would be true even if there is considerable variation in body size within these orders, because the interordinal variation overwhelms the intraordinal variation. This same principle applies, albeit to a lesser extent than in this example, to the data sets I analyzed. Thus the reader should not be surprised if the percent variance for some variables is high at levels other than the genus.

Another consideration when interpreting nested analyses of variance is that some variables are probably more subject to species selection than others. Of the variables in my data set, I expect variation in stratigraphic range to be the best indicator that species selection might be rapid. The reason for this is simple: of all the variables in my data set, stratigraphic range is the only one with a necessary connection to extinction. RS variation should also set the stage for species selection, since species of very small RS are likely to become extinct soon. Litter size could also affect population size; and hence, probability of extinction, albeit less so than RS because the magnitude of variation in litter size is much less than in RS. Although body size has been suggested to correlate positively with extinction probability, this relation might be important only when the species contrasted are of widely disparate body sizes. Thus variation in HBL might be expected to correlate more strongly in higher than in lower taxa because there is so much more variation in HBL at higher taxa. For example, the size difference between voles (*Microtus*) and mammoths (*Mammuthus*) could differentially affect their extinction probabilities, but size differences between two species of *Microtus* might not.

The variable in my data set that probably is most weakly correlated with extinction probability is length of lactation. Although there might be a negative correlation between length of lactation and reproductive rate, the relationship at lower taxonomic levels is probably too weak to substantially affect extinction probability. This is probably at least in part because of the crudeness and inaccuracy of measurement of this variable. In any case, Predictions 4.1, a-c, are that stratigraphic range and RS will have large variances among the species within genera, that litter size and HBL will have somewhat smaller intrageneric variances, and length of lactation will have even less. I will now explain why I find intrageneric variation is particularly interesting.

Although extinction can occur at any taxonomic level, the greater age of higher taxa (Rensch 1960) suggests that extinction is less common at higher levels. I therefore expect extinctions of species to be more common than extinctions of higher taxonomic levels. The lowest taxonomic level in my analysis that is more inclusive than species is the genus; hence, I infer a greater frequency for species selection at the level of genus than for extinction of higher levels. To put it more precisely, there have been more extinctions of species than of genera, families or orders. Hence, I predicted that characters highly correlated with probability of extinction will exhibit large variation at the level of genus.

The shotgun model also suggests that monospecific genera are often the residue of extinctions among speciose genera. This suggests that if we could somehow remove the short-lived species from speciose genera, that the remaining species would resemble monospecific genera. I was unable to address this question rigorously, but I was at least able to compare the variances of the two types of genera. Prediction 4.2 is thus that the variance among monospecific genera is similar to that among speciose genera when variation among the species in each speciose genus is controlled for statistically.

The shotgun model implies that with a greater passage of time there is more opportunity for species selection. Since higher taxa have greater stratigraphic ranges than lower taxa (Rensch 1960; Van Valen 1973), we can infer that they have, on average, been subject to more species selection than the lower taxa contained within them. Thus the relative importance of natural vs. species selection could vary with taxonomic level, resulting in different patterns of association among variables. Thus Prediction 4.3 was that signs of association will tend to differ among taxonomic levels, and the differences will be greater with widely-disparate levels than among taxa that are fewer levels apart.

Materials and Methods

The nested analysis of variance technique used in this chapter is available on the SAS statistical package (SAS Institute 1985). The sources of data were described in Chapter I, and the variables used were those for which sample sizes were largest, and which were generally comparable (except for stratigraphic range) between Australia and North America. All of the nested analyses of variance used only genera with more than two species. Some of the so-called monospecific genera used to test Prediction 4.2 were not monospecific in the strict sense but were the only Nearctic species in the genera. For example, the elk (*Cervus canadensis*) was considered to be monospecific even though there are several species of Old World *Cervus*. My rationale for this is that the Old World *Cervus* belong to a different evolutionary theatre; and hence, are irrelevant to studies of Nearctic mammal evolution.

To compare the variances of monospecific and speciose genera, I used an F statistic, with Satterthwaite's Formula to calculate the degrees of freedom (Milliken and Johnson 1984). The mean square for the genera, mean square error, coefficients of expected mean square, sample size and variance for monospecific genera, were all calculated by the PROC NESTED and PROC MEANS options of the SAS statistical package. Since I had no reason to expect either type of genus to have greater variance, I conducted two-tailed tests. One might, however, hypothesize that monospecific genera actually have greater variances, for reasons given in the next chapter. Therefore I also calculated the F statistics assuming a one-tailed test.

For my comparison of selection at different taxonomic levels, several taxonomic levels were examined. The most-inclusive taxonomic level available for mammals is the class itself. Hence, the data set for the most-inclusive group included all the species in my data set. The lowest taxonomic level appropriate to this analysis is the genus; hence, for this level I used species grouped by genera.

Between the levels of genus and class are order and family; hence, these were also examined. Other intermediate taxonomic levels (e.g., suborder and superfamily) were not used; these levels are not obligate and not all of them exist for all taxa.

I compared the associations of variables among the levels by means of Kendall's tau-b correlation and nested analysis of variance. There are sometimes problems in making quantitative comparisons of different taxonomic levels (Pagel and Harvey 1988). Furthermore, since statistical methods to compare signs of association are not well established, my assessment should be considered exploratory and not definitive. My method for assessing Prediction 4.3 was to tally discordances of sign of association between variables at the class and genus level. I noted changes in sign of association between levels one, two and three steps apart in the taxonomic hierarchy. Levels one step apart were genus and family, family and order, and order and class. Levels two steps apart were genus and order and family and class. Levels three steps apart were genus and class. I hypothesized that the number of discordances would correlate positively with the number of steps between levels. My evaluation was extremely crude in that it ignored differences in degree and only detected differences in direction of association. I therefore expected very few differences under the null model that the signs of association will not differ depending upon taxonomic level.

I excluded from consideration levels for which the associaton was not statistically significant, thereby greatly reducing my sample size. In all cases I kept the comparisons within lineages; for example, I compared the signs of association for variables of ground squirrels of the genus Spermophilus to signs for the order Rodentia, not the order Carnivora.

To render this investigation more robust I replicated it on another continent, Australia, using data from Appendices E and F (the sources for which were listed in Chapter II). The basic methodology was the same as for North America but fewer variables were available for the Australian study. To compare the various taxonomic levels, I used a nested analysis of variance technique, as described by Bell (1989). The highest level of classification that I used separated mammals into monotremes, marsupials and eutherians, which are not strictly speaking at the same taxonomic level, since the latter two taxa belong to a different subclass from the monotremes. However, these three taxa are well-differentiated and recognizable; hence, for the present purposes will be considered to be equivalent in rank. The other taxonomic levels used were order, family, genus and species; for marsupials I followed Strahan (1983) in recognizing two orders of marsupials, Diprotodonta and Polyprotodonta.

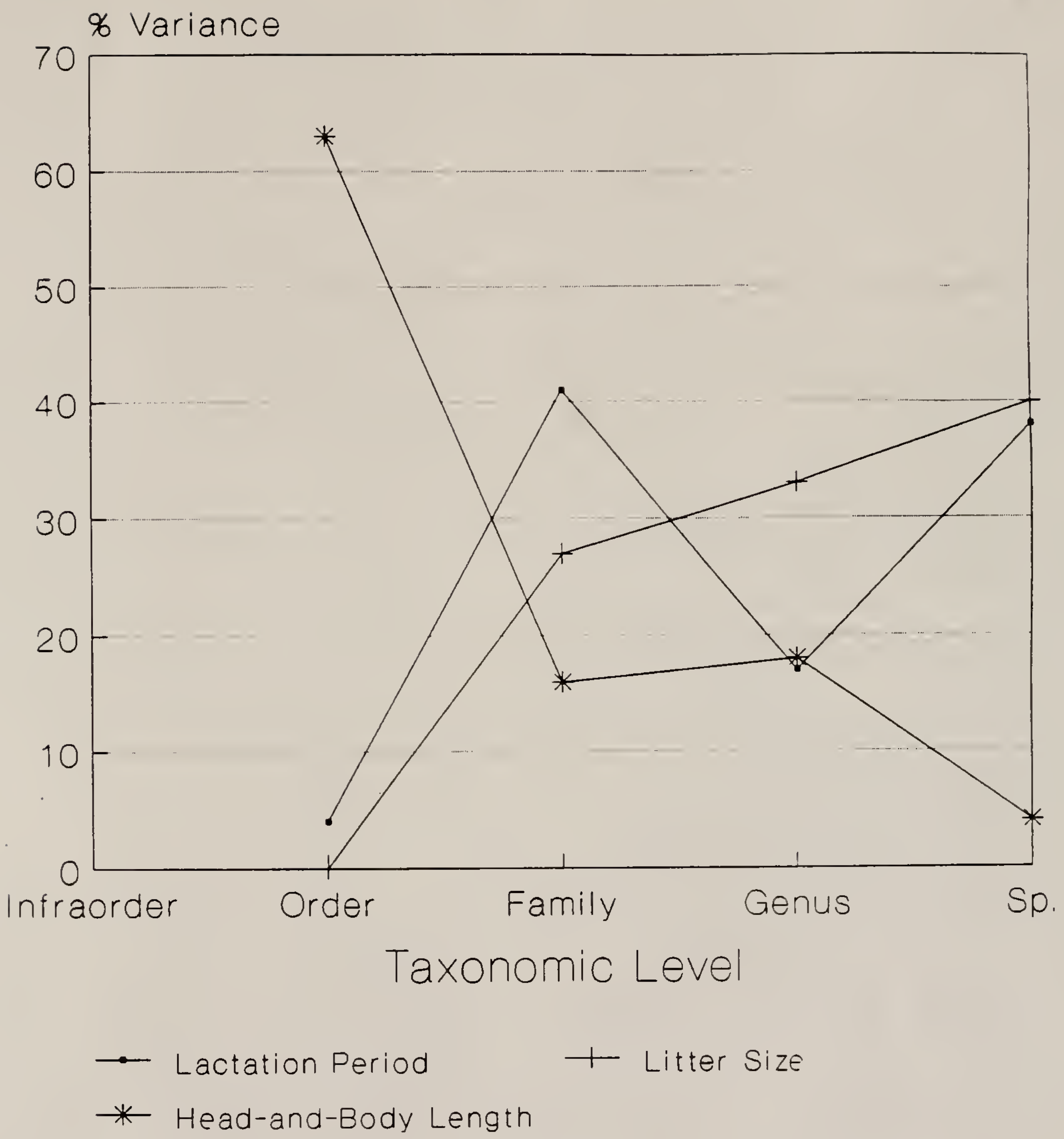
Results

The percents of variation associated with each taxonomic level are shown in Figs. 4, 1-3. The _F_ tests comparing monospecific and speciose genera are summarized in Table 4-1. Although I assumed the tests to be two-tailed, the same statistical conclusions were reached when one-tailed tests were performed. There were no significant differences except for the variable lactation period, for Australian mammals, between monospecific and speciose genera. Therefore only the results of the one-tailed tests are shown.

The correlation coefficients for comparisons of processes at different taxonomic levels, for North American species, are shown in Table 4-2. Table 4-2 includes only statistically significant ($\underline{P} < 0.05$) coefficients. A comparison of signs of association of genus and class is shown in Table 4-3, where only significant ($\underline{P} < 0.05$) associations are listed. Briefly, a large proportion (seven out of fifteen or 46.76%) of the associations differ in sign between the level of class and the level of genus.

Although even if the same processes occurred at both levels we might expect a small number to differ in sign by chance alone, the large proportion that do differ in sign is

Figure 4-1. Results of nested analysis of variance (ANOVA) for North American mammals. Variables included lactation period, head-and-body length and litter size. All data were log-transformed.



North America

Figure 4-2. Results of nested analysis of variance (ANOVA) for North American mammals. Variables included stratigraphic range and RS. All data were log-transformed.

North America (cont.)

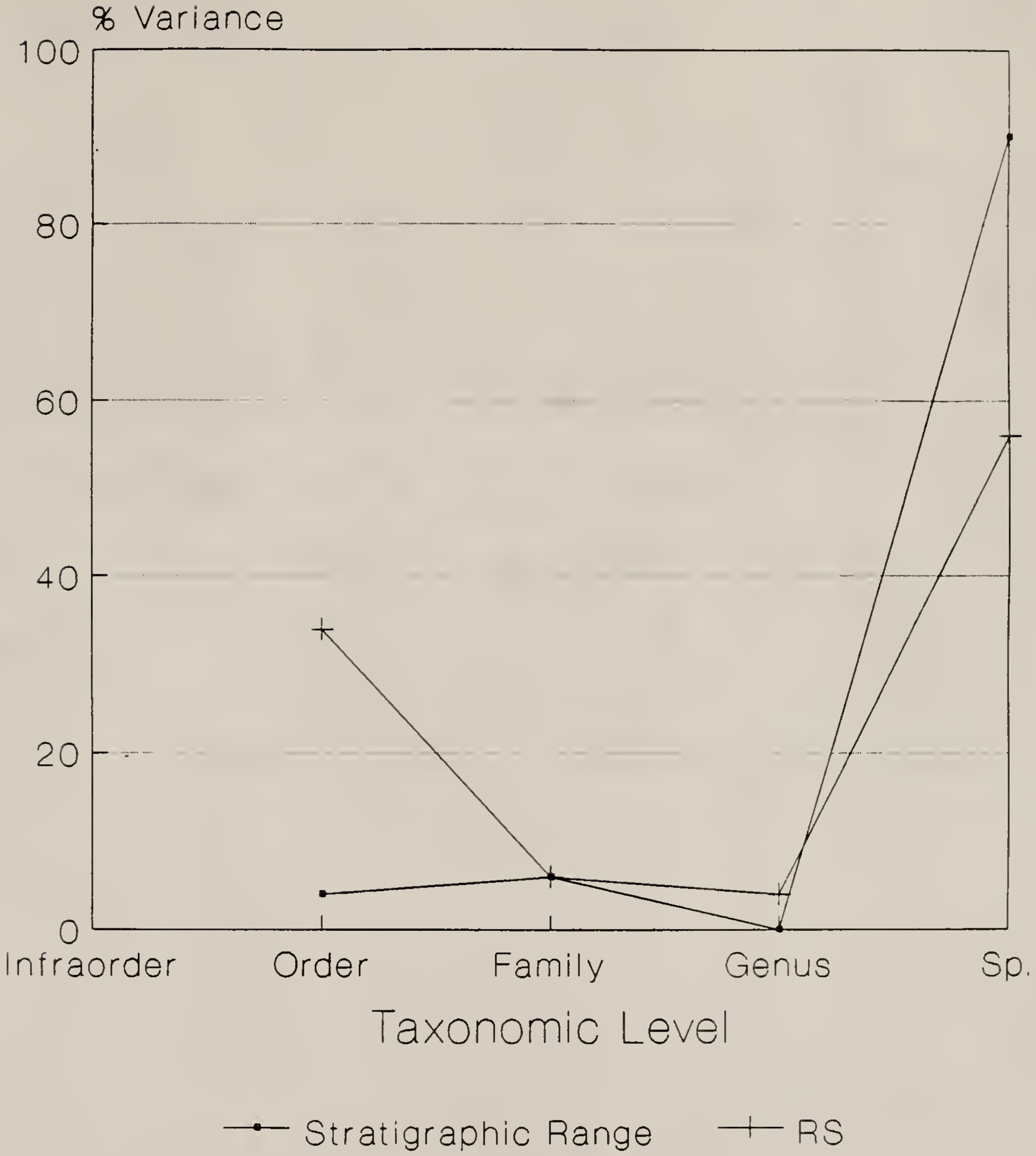


Figure 4-3. Results of nested analyses of variance (ANOVA) for Australian mammals. Variables included geographic range size, head-and-body length, lactation period and litter size.

Australia

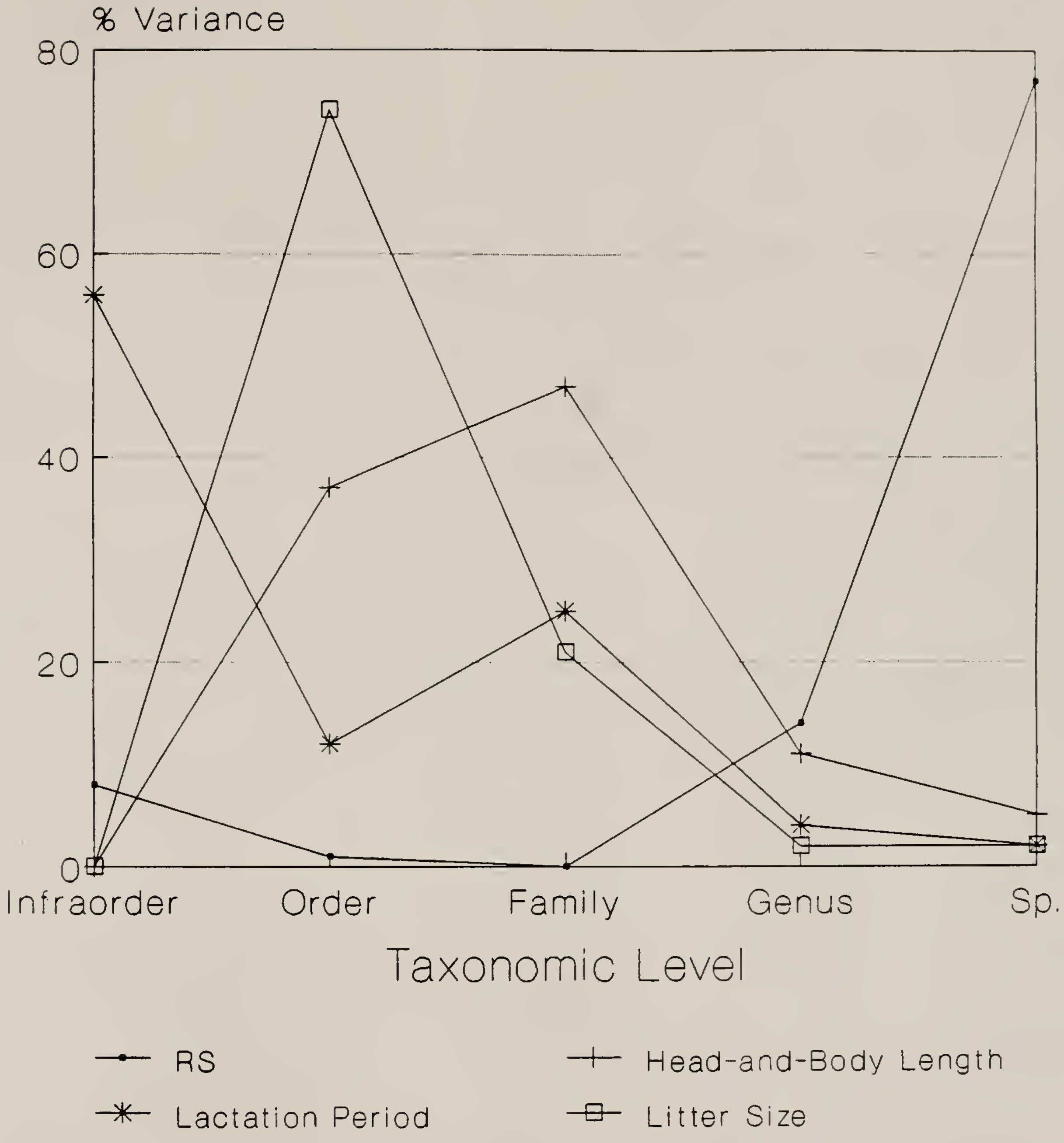

% Variance
80
60
40
20
0
Infraorder
Order
Family
Genus
Sp.
Taxonomic Level
RS
Head-and-Body Length
Lactation Period
Litter Size

Table 4-1. Tests for the equality of variance of variables for monospecific and speciose genera.

Variable*	Continent	$F_{0.025}$	F_s
HBL	North America	2.206	0.200
Lactation Period	North America	13.922	0.132
RS	North America	2.003	1.413
Litter Size	North America	3.392	0.653
HBL	Australia	4.051	0.662
Lactation Period	Australia	1.709	40.473
RS	Australia	3.120	2.277
Litter Size	Australia	2.180	0.460

[*] Data were from Appendices A-F, and were natural-log-transformed. These were two-tailed tests, so the probabilities were $a/2$ or 0.025. These were approximate values, taken directly and without interpolation from a table for the F distribution. The F_s column contains variance ratios calculated for the actual data. $F_s > F_{0.025}$ indicates that monospecific genera were significantly more variable than speciose genera.

Table 4-2. Significant ($\underline{P} < 0.05$) Kendall's tau-b correlations for North American mammals.

Variables	Correlation Coefficient	Taxon
HBL, Birth Weight	0.6671	Insectivora
Eurytopy[a], Gestation Period	-0.6901	Insectivora
Gestation Period, Density	-1.0000	Insectivora
HBL, Gestation Period	0.5353	Insectivora
Litter Size, Birth Weight	-0.6923	Insectivora
Eurytopy[a], Birth Weight	-0.8099	Insectivora
Litter Size, RS	0.3807	Insectivora
Food Abundance[b], RS	0.3210	Insectivora
HBL, Gestation Period	0.3775	Carnivora
HBL, Litter Size	-0.3205	Carnivora
HBL, Density	-0.4403	Carnivora
Litter Size, Density	0.4088	Carnivora
HBL, Birth Weight	0.8618	Carnivora
Litter Size, Birth Weight	-0.4176	Carnivora
Density, Birth Weight	-0.5340	Carnivora
HBL, Gestation Period	0.5273	Artiodactyla
HBL, Litter Size	-0.6242	Artiodactyla
HBL, Birth Weight	0.8889	Artiodactyla
HBL, EQ[c]	-1.0000	Artiodactyla
Gestation Period, EQ[c]	-1.0000	Artiodactyla
Polymorphism, Heterozygosity	0.6500	Artiodactyla
RS, Eurytopy[a]	0.2475	Rodentia
Lactation Period, Growth Rate	0.6260	Rodentia
Birth Weight, Growth Rate	0.6827	Rodentia
Food Abundance[b], Growth Rate	-0.3176	Rodentia
HBL, Growth Rate	0.6985	Rodentia
Polymorphism, Heterozygosity	0.7550	Rodentia
HBL, Birth Weight	0.7415	Rodentia
Gestation Period, Birth Weight	0.4927	Rodentia
Lactation Period, Birth Weight	0.3235	Rodentia
Gestation Period, Lactation Period	0.4614	Rodentia
HBL, Lactation Period	0.3895	Rodentia
Gestation Period, Density	-0.3298	Rodentia
HBL, Food Abundance[b]	-0.2763	Rodentia
Gestation Period, Litter Size	-0.2184	Rodentia
HBL, Gestation Period	0.4476	Rodentia
HBL, Gestation Period	0.7182	Canidae
HBL, Birth Weight	1.0000	Canidae
HBL, Growth Rate	1.0000	Canidae
HBL, Birth Weight	0.7857	Mustelidae
Litter Size, Birth Weight	-0.7413	Mustelidae
Eurytopy[a], Birth Weight	-0.7370	Mustelidae
HBL, Gestation Period	0.8411	Leporidae
HBL, Density	-0.5714	Leporidae
Gestation Period, Density	-0.7333	Leporidae

Table 4-2--continued.

Variables	Correlation Coefficient	Taxon
HBL, Gestation Period	0.5610	Heteromyidae
HBL, Litter Size	0.3806	Heteromyidae
Gestation Period, Litter Size	-0.6405	Heteromyidae
HBL, Birth Weight	0.8668	Heteromyidae
Gestation Period, Eurytopy[a]	-0.5057	Heteromyidae
Gestation Period, Birth Weight	0.6405	Heteromyidae
Eurytopy[a], RS	0.3328	Heteromyidae
Litter Size, Polymorphism	-0.7947	Heteromyidae
Polymorphism, Heterozygosity	0.6269	Heteromyidae
Lactation Period, Growth Rate	1.0000	Heteromyidae
HBL, Gestation Period	1.0000	*Lepus*
Gestation Period, RS	-1.0000	*Lepus*
HBL, Food Abundance[b]	-0.5561	*Microtus*
HBL, Birth Weight	0.8095	*Microtus*
HBL, RS	0.3672	*Microtus*
Food Abundance[b], RS	-0.4363	*Microtus*
HBL, Birth Weight	0.7760	*Dipodomys*
Litter Size, Polymorphism	-0.7947	*Dipodomys*
Litter Size, RS	-0.5930	*Neotoma*
Gestation Period, Eurytopy[a]	0.8890	*Sciurus*
Eurytopy[a], Density	-0.8890	*Sciurus*
Gestation Period, RS	-1.0000	*Perognathus*
HBL, Birth Weight	1.0000	*Spermophilus*
HBL, Growth Rate	0.5714	*Spermophilus*
Food Abundance[b], RS	0.4457	*Spermophilus*
Density, RS	-0.5290	*Spermophilus*
HBL, Gestation Period	0.6506	Mammalia
HBL, Litter Size	-0.1797	Mammalia
HBL, Food Abundance[b]	-0.1823	Mammalia
HBL, Birth Weight	0.8233	Mammalia
HBL, Eurytopy[a]	0.1190	Mammalia
HBL, Density	-0.4536	Mammalia
HBL, Lactation Period	0.4471	Mammalia
HBL, Home Range Size	0.6266	Mammalia
HBL, RS	0.2654	Mammalia
HBL, Growth Rate	0.8511	Mammalia
Gestation Period, Birth Weight	0.7034	Mammalia
Gestation Period, RS	0.2328	Mammalia
Gestation Period, Litter Size	-0.3524	Mammalia
Gestation Period, Density	-0.5364	Mammalia
Gestation Period, Lactation Period	0.5175	Mammalia
Gestation Period, Growth Rate	0.6847	Mammalia
Gestation Period, Home Range Size	0.6043	Mammalia
Litter Size, Density	0.2032	Mammalia
Litter Size, Birth Weight	-0.3026	Mammalia

Table 4-2--continued.

Variables	Correlation Coefficient	Taxon
Litter Size, Growth Rate	-0.2049	Mammalia
Litter Size, Home Range Size	-0.2342	Mammalia
Food Abundance[b], Density	-0.2658	Mammalia
Food Abundance[b], Lactation Period	0.1667	Mammalia
Food Abundance[b], Birth Weight	-0.1703	Mammalia
Food Abundance[b], RS	0.1112	Mammalia
Food Abundance[b], EQ[c]	0.3685	Mammalia
Food Abundance[b], Home Range Size	0.2577	Mammalia
Eurytopy[a], RS	0.2934	Mammalia
Eurytopy[a], Growth Rate	0.3044	Mammalia
Density, Lactation Period	-0.3903	Mammalia
Density, Birth Weight	-0.4146	Mammalia
Density, RS	-0.3935	Mammalia
Density, Growth Rate	-0.4823	Mammalia
Density, Home Range Size	-0.6631	Mammalia
Lactation Period, Birth Weight	0.4735	Mammalia
Lactation Period, RS	0.2908	Mammalia
Lactation Period, Growth Rate	0.4808	Mammalia
Lactation Period, Home Range Size	0.3625	Mammalia
Birth Weight, RS	0.2445	Mammalia
Birth Weight, Growth Rate	0.8351	Mammalia
Birth Weight, Home Range Size	0.5419	Mammalia
RS, Growth Rate	0.3440	Mammalia
RS, Home Range Size	0.4604	Mammalia
Growth Rate, Home Range Size	0.6957	Mammalia
Polymorphism, Litter Size	0.6485	Mammalia

[a] Defined as in Table 2-1.

[b] Defined as in Table 2-1.

[c] Encepahization Quotient.

Table 4-3. Significant ($p < 0.05$) signs of association of variables for North American mammals.

Variables*	Sign for Class	Sign for Genus (Genus)
HBL, Gestation Period	+	+ (*Lepus*)
HBL, Litter Size	-	+ (*Perognathus*)
HBL, Food Abundance	-	- (*Microtus*)
HBL, Birth Weight	+	+ (*Spermophilus*); - (*Dipodomys*)
HBL, RS	+	+ (*Microtus*)
HBL, Growth Rate	+	+ (*Spermophilus*)
Gestation Period, Eurytopy	+	+ (*Sciurus*)
Gestation Period, Birth Weight	+	- (*Microtus*)
Gestation Period, RS	+	- (*Perognathus*); - (*Lepus*)
Food Abundance, RS	+	+ (*Spermophilus*); - (*Microtus*)
Polymorphism, Litter Size	+	- (*Dipodomys*)
Density, RS	-	- (*Spermophilus*)

* Eurytopy and Food Abundance are as defined in Table 2-1.

surprising. An assessment for Australian mammals was not conclusive, perhaps because there were too few analyses.

Further tests on North American mammals with one and two taxonomic levels revealed that none of ten tests one level apart and two of 22 tests two levels apart had opposite signs of association at the levels compared. Incorporating the results for tests comparing genera and class, which are three levels apart (i.e., genus to family, family to order and order to class), we see that the amount of discordance at one, two and three levels of difference was 0%, 9.1% and 46.7%, respectively. Although the number of significant tests for each category of difference in level was too small to warrant defintive statements, it does appear that the more disparate the taxonomic levels, the more likely they are to exhibit different signs of association.

The statistically significant ($\underline{P} < 0.05$) coefficients associated with the Australian tau-b analyses are shown in Table 4-4. There was one correlation significant at both the level of class (i.e., among all the mammals taken as a whole) and for genera.

Discussion

As explained in the Introduction, an understanding of magnitudes of variance at different taxonomic levels is improved when basic natural history of the organisms is considered. For example, variation in RS and HBL is

Table 4-4. Significant ($p < 0.10$) Kendall's tau-b correlations for Australian mammals.

Variables*	Taxon	Correlation	P Value
Eurytopy, RS	_Antechinus_	0.55748	0.0403
Density, RS	_Antechinus_	0.61865	0.0222
Eurytopy, RS	_Macropus_	0.45693	0.0497
Density, Eurytopy	_Pseudomys_	0.53849	0.0131
Gestation, Litter Size	_Pseudomys_	0.81763	0.0097
Food Abundance, Litter Size	_Pseudomys_	0.66720	0.0195
Eurytopy, RS	Mammalia	0.46993	0.0001
Litter Size, Mass	Mammalia	-0.78100	0.0001
Density, Home Range Size	Mammalia	-0.61905	0.0509
Density, HBL	Mammalia	-0.35317	0.0187

* Eurytopy and Food Abundance as in Table 2-1. Small sample sizes for some variables prompted me to use an alpha level of 0.10.

considerable at the level of order. This is entirely in accord with what is known about these taxa. First let us consider HBL. Orders of Nearctic mammals have restricted size ranges, such that insectivores are small, artiodactyls are very large, carnivores tend to be medium-sized, lagomorphs slightly smaller than carnivores, and rodents usually small or medium in size. Although the previous statements are just generalizations, the generalizations are real enough to account for a large fraction of the size variation in Nearctic mammals. By contrast, order explains somewhat less of the size variation in Australian mammals. Although monotremes and murid rodents are rather sharply delimited in body size, the two most speciose orders, Polyprotodonta and Diprotodonta, overlap greatly in body size and are poorly distinguished on that basis. On the other hand, families of Australian mammals are more sharply differentiated in size; hence, there is large variation among families relative to that among units at other taxonomic levels. Litter size of Australian mammals tends to be explained well at the ordinal level, however; rodents and polyprotodonts have large litters and diprotodonts tend to have small litters. Although I did not include trophic level in these analyses, the ordinal level also discriminates well between the primarily animalivorous polyprotodonts and the primarily herbivorous diprotodonts and rodents. The point to be made from the foregoing discussion is that high variance at a taxonomic level is often an indication that taxa at that level are relatively distinct from one another, not that there is considerable variation within each order. To assess the variation within a taxonomic level it is necessary to look at the next lowest level. Thus to assess the variance within the genera we must look to the level of species.

As predicted (Prediction 4.1a,b), the intrageneric variance in stratigraphic range and RS are enormous. There is clearly enough variation in these variables to facilitate extinction and species selection. One could infer from the large intrageneric variation in stratigraphic range that selection is intensively weeding out species within genera--just as I posited for the shotgun model.

As expected, the other variables do not provide as much support for the shotgun model as do stratigraphic range and RS. As predicted (Prediction 4.1c), variance in litter size increases from genus to species, but less markedly than stratigraphic range and RS. Period of lactation increases from genus to species in North America but not in Australia, whereas HBL decreases on both continents. The overall trend, then, is as expected; variables purported to be highly correlated with extinction show large variation within genera relative to the variation between genera. Variables not highly correlated with intrageneric extinction do not show these strong trends. The shotgun model posits an explosive radiation in species followed by many intrageneric extinctions. Large variations in stratigraphic range are consistent with numerous extinctions resulting in a few long-lived species, whereas large variations in RS could be considered to indicate incipient extinction as populations of species of small RS dwindle.

Similarity in variance among monospecific genera and speciose genera, correcting for intrageneric variation (Prediction 4.2), are consistent with the notion that monospecific genera are often surivors of extinctions in speciose genera.

For the North American data, the difference in sign of association between variables at the genus level and class level is not readily understood by associating it with any conventional natural history variable, although it does appear to be related to time elapsed since origin of taxa.

Hence, I suggest that the differences between signs of association at different taxonomic levels are most parsimoniously attributed to differences in age between them. Since the turnover of higher taxonomic levels is lower than for lower levels, this implies that for such a difference to be detectable the selection has been occurring for a much longer time at higher taxonomic levels. Furthermore, differences in association between genus and class (which are three levels apart) must have even more ancient roots.

Furthermore, the inverse relation between number of intervening taxonomic levels and concordance in sign of association suggests that there is an ecological reality to the taxonomic hierarchy conventionally used by biologists. Adjacent taxonomic levels are more similar to one another in sign of association among variables than they are to levels one or more steps away in the hierarchy. Ecology is well known to reflect phylogeny to a certain extent; what I suggest is that it does so in a rarely recognized way (but see Bell (1989)).

Although all of the Australian analyses agreed in sign between taxonomic levels, it would be premature to draw conclusions from so small a sample. Thus the Australian analyses could not be said to either confirm or deny my hypothesis that taxonomic levels exhibit opposing signs of relationship among variables.

Good taxonomy is a prerequisite to all of my analyses to a greater or lesser extent. However, a tendency to either lump or split genera would have obscured distinctions between monospecific and speciose genera such that I would have been unlikely to detect the differences that I did in fact find. Thus even if taxonomists have biases, these are unlikely to have interfered with the present study. Furthermore, by using widely-disparate levels in my genera/class comparison I virtually eliminated the importance of misclassifying taxa to one level or the other.

Factors such as anthropogenic disturbance will almost certainly cause us to underestimate the extent of higher-level selection. Nevertheless, there do appear to be real differences in direction of selection at disparate taxonomic levels. Even the reported high proportion of discordance is an underestimate because it does not include the North American genus _Peromyscus_; in this genus there is a negative correlation between HBL and RS (Glazier 1980) which is opposite to the sign of association for the class. So it seems that we have at least a partial answer to one of the questions raised in the first chapter, namely, Why are some of the relations between variables in _Peromyscus_ opposite in direction to the class as a whole? The answer, I believe, is simply that natural selection predominates in determining the interspecific trends in _Peromyscus_, but that at the level of class higher-level selection is also at work.

Reviewers have suggested that the methodology I employed does not take into account the possibility that some of the many tau-b analyses are likely to be significantly different by chance alone. Unfortunately, there does not seem to be any simple method to control for multiple comparison error rate for the type of analyses I performed. One possibility is to decrease the alpha level and then retally my discordances. However, such corrections of alpha level are usually used to account for a _general_ significant difference in sign of association. To my knowledge, there is no ready method to correct for multiple comparison error rate when comparing signs of association among variables, and as noted above, there are problems in making quantitative comparisons of slopes of regression lines between taxonomic levels. My conclusions therefore are only tentative. However, the greater concordance between adjacent than disparate taxonomic levels is difficult to explain as being due to chance, since the trend is monotonic over several changes in taxonomic level. Furthermore, one of the potential problems with multiple comparisons was not applicable to this study. Although a high multiple comparison error rate reduces the confidence we can attach to the significance of any given test, I did not attempt to specify which comparisons would be significant. I was interested in the overall number of associations that were concordant from one level to the next, not in finding which associations were significant.

I have left until last what is probably the most important criticism of my taxonomic analyses. In a hierarchy of nested sets, we might expect a subset to be more similar to the set that is just one step above it in the hierarchy, than to the sets that are even more inclusive. The reason for this is that autocorrelation is higher in adjacent taxa because the autocorrelated taxa make up a larger fraction of a small set than of a larger, more inclusive set. For example, consider foxes of the genus *Vulpes*. The foxes in this genus make up a larger fraction of the family Canidae than they do of the order Carnivora; hence, variables for Vulpes might be expected to correlate more highly with the family Canidae (of which they are a large part), than for the order Carnivora (of which they are but a small part).

This might not, however, be a crippling problem for the present investigation. Note that I examined changes in sign of association among variables, not the variables themselves. Changes in association among variables often prove more useful in understanding processes than do the variables themselves; for example, changes in the ratio of two variables, namely surface area and body mass, explain how metabolic rate changes with size. By contrast, neither body mass or surface area alone are explanatory of metabolic rate, and are used as indices of metabolic rate because a relationship is (often implicitly) assumed. Thus in many cases it is the relationship among variables, not the variables themselves, that is most interesting.

Furthermore, much of predictive biology assumes that qualitatively similar processes generally occur at various taxonomic levels. For example, we might expect a positive correlation between body length and weight to occur within genera and families as well as within the class as a whole, even if the relation differs quantitatively from level to level. I have used this "uniformitarian" perspective as a null model. Specifically, my null hypothesis was that associations at all taxonomic levels should be at least *qualitatively* similar--i.e., similar in sign. Proponents of alternative models thus bear the burden of proof of explaining why an association among variables should be qualitatively dissimilar among the various taxonomic levels, and why the dissimilarity should increase with the number of intervening taxonomic levels. The shotgun/logistic model is one such explanation.

In general, then, the major prerequisites for species selection are met. In the following chapters I will examine what has resulted from the process.

CHAPTER V

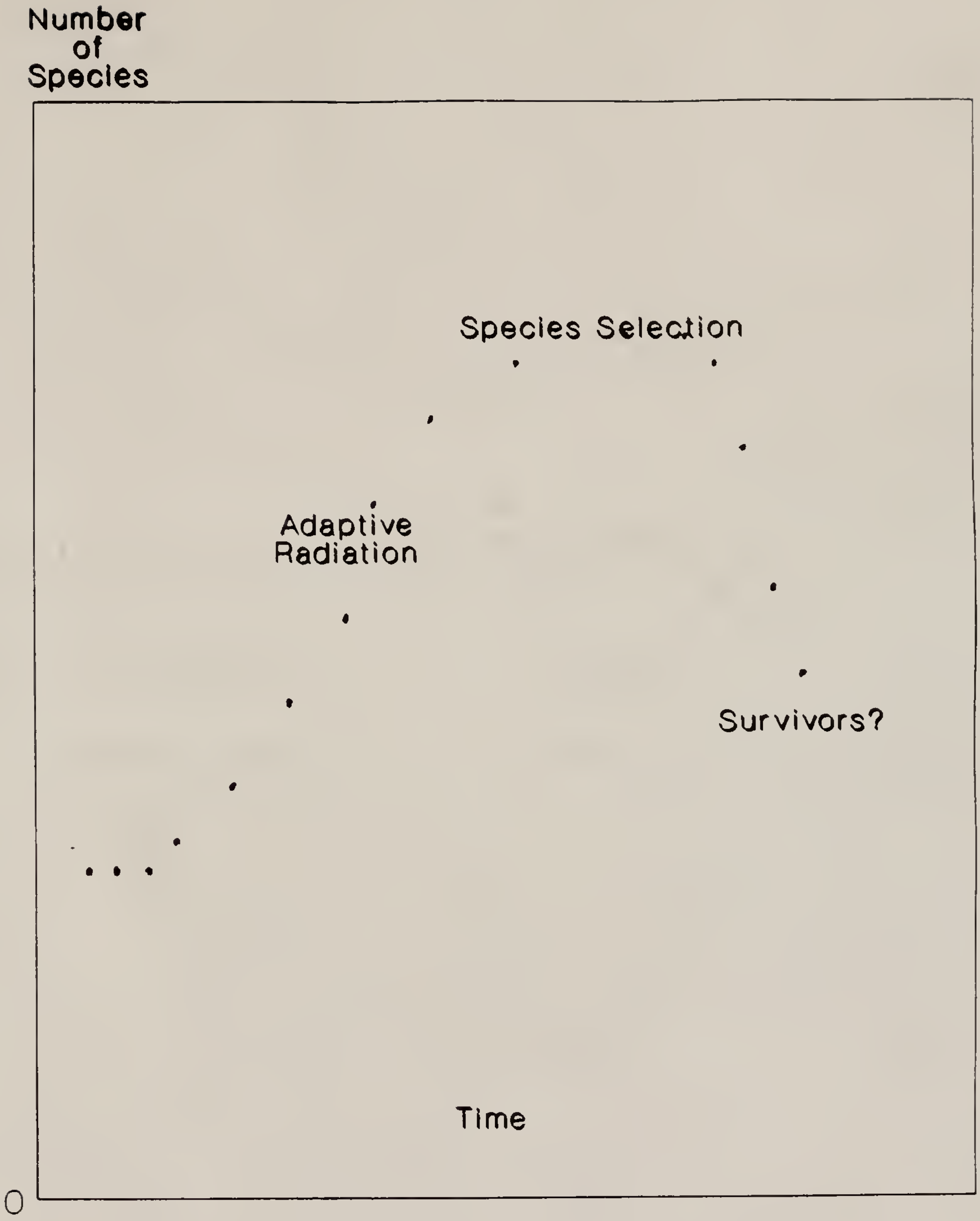
MONOSPECIFIC VS. SPECIOSE GENERA

Introduction

In Chapter IV I used a comparison of the variance in monospecific vs. speciose genera to assess whether the prerequisites for selective extinction were met. In the present chapter I will show that a comparison of monospecific and speciose genera can also be used to make predictions about the attributes possessed by species that survive adaptive radiation, although herein I will compare central tendencies (means or medians) rather than variances.

The shotgun and logistic models discussed in Chapter III suggest that only a few species survive adaptive radiations (Fig. 5-1). Furthermore, species surviving adaptive radiations will differ from species that perish in adaptive radiations. Monospecific genera might be such survivors of adaptive radiations, whereas speciose genera could be considered to be still in the process of adaptively radiating. A dichotomy can be hypothesized for monospecific vs. speciose genera under the assumption that the latter have not yet passed through an extinction barrier. Although I have posited that monospecific genera are in some sense better survivors than are species from

Figure 5-1. Posited changes in species richness of a typical higher taxon through phases in the adaptive radiation process.


Number of Species
Species Selection
Adaptive Radiation
Survivors?
Time
0

Although I have posited that monospecific genera are in some sense better survivors than are species from speciose genera, I do not mean to imply that a species in a monospecific genus must be the only survivor of the adaptive radiation of a speciose genus. Although this could happen, a monospecific genus might also have always been the only species in its genus. The important point here is that it is a long term survivor. Of course all species have a short life span in terms of the geological time scale, but on a smaller time scale the variation is considerable (e.g., Van Valen 1973; Kurten and Anderson 1980, Appendix 2).

If monospecific genera are indeed survivors of adaptive radiations then they would be expected to have greater stratigraphic ranges than species from speciose genera. Furthermore, if monospecific genera do survive longer it is probably because they possess adaptations or values for characters, lacking in most species from speciose genera. Monospecific genera are also predicted by the shotgun and logistic models to differ from species in speciose genera in the same way that *K*-strategist species differ from *r*-strategist species.

Prediction 5.1 is thus that monospecific genera have greater stratigraphic ranges than species from speciose genera. I tested this using longevities of species of North American mammals that lived at some time in the interval from the Hemphillian (Miocene) to the Recent.

I then wondered whether monospecific genera, as survivors of higher-level extinction, have converged on a more limited set of characteristics than have species less subject to these agents. Perhaps monospecific genera possess unusual characteristics that render them more resistant to extinction than species from speciose genera. One might then predict that species from speciose genera will exhibit more variation than species from monospecific genera. Unfortunately this hypothesis was impractical to test statistically. This did not, however, preclude an examination of the extreme values for the two groups. Thence, Prediction 5.2: Monospecific genera possess more unusual characteristics than species from speciose genera. Prediction 5.3, taken from the shotgun and logistic models, is that monospecific genera will differ from species in speciose genera in the same direction that *K*- strategist species differ from *r*- strategist species. Specifically, it predicts monospecific genera will be larger, have longer gestation periods, and have smaller litters. *K*- strategist species are normally considered to differ from *r*- strategist species in several other respects as well, but these other variables were not included in my data set.

Materials and Methods

I tested the hypothesis that species from monospecific genera survive longer (Prediction 5.1) by using stratigraphic ranges for species of North American mammals from the Hemphillian (Miocene) to the Recent. Using stratigraphic ranges for species from Appendix 2 of Kurten and Anderson (1980), I compared the longevities of monospecific vs. speciose genera by means of a Wilcoxon signed-ranks test. To clarify the comparison I excluded genera with two species, so that the actual comparison was of genera with one species and genera with more than two species.

I attempted to do a similar test on Australian mammals but ran into insurmountable difficulties. The most complete list of fossil mammal species of Australia was that of Archer *et al*. (1984). Because this list does not include absolute dates, but only the epochs in which the species lived, I attempted to quantify the age of the species by noting in how many epochs it was found. Unfortunately, the bulk of the species lived in a single epoch, and none lived in more than two epochs; hence, the range of variation upon which to conduct an analysis was very small. Furthermore, the list was not usually specific about what portion of each epoch the species lived in; hence, species that lived at the very end of one epoch and the very beginning of the next would be scored as longer-lived than one that spanned an entire epoch, because the former would be considered to live in two epochs and the latter just one. Finally, epochs differ in length; hence, species could have the same score but unequal lifespans because one lives in a longer epoch.

It is thus apparent that the Australian data are not sufficiently refined for such an analysis as I conducted on North American species.

Above I suggested that species from monospecific genera might be more unusual than most species from speciose genera (Prediction 5.2). Mathematically, "uniqueness" might be manifested by high variance. The reader may recall that in the previous chapter monospecific genera were not found to vary more, in at least four characters (HBL, lactation period, RS and litter size), than speciose genera. Superficially this would seem to suggest that monospecific genera are not more unusual than species from speciose genera, but I believe this to be a premature conclusion.

Firstly, variance is not the only statistical parameter useful in assessing uniqueness. At least two other parameters, namely the mean (or median) and the range, are also useful. It is, for example, quite possible for two populations to have similar variances but different means, and if one adds or subtracts a constant value to every datum, the variance will remain unchanged even though the mean shifts. Thus, for example, although the median body length of Mesozoic reptiles and Pleistocene mammals is probably very similar to that of Holocene mammals, the frequency of species from the Holocene fauna that fall in the upper size ranges is dramatically less than for the Pleistocene and Mesozoic.

The outliers responsible for a range in values might also be of interest to someone investigating uniqueness. Statisticians often find outliers to be the most intriguing data points, perhaps because they could indicate startling departures from the typical pattern. Since my analyses of variance did not investigate either outliers or differences in mean value, they could seriously underestimate uniqueness.

Another major reason my previous analyses were inadequate for assessing uniqueness is thay they included information for only four variables. Some species with unexceptional values for the variables I used would nevertheless probably be considered to be unusual in either structure or behavior by laymen and scientists alike. I cite as examples giraffes, armadillos, star-nosed moles, gibbons, echidnas and the platypus. None of these species are outliers for the four variables studied previously, yet they could all be easily separated from other mammals by morphological or behavioral criteria. Thus I could more comprehensively assess uniqueness by investigating more variables. Unfortunately the logistics of a comprehensive study of uniqueness are formidable. This is because uniqueness, in the sense it is used herein, is a nebulous quality, a gestalt that is difficult to quantify without measuring an enormous number of variables. As Ehrenfeld (1989) opines, scientists have lost fascination with the specific in favor of a preoccupation with the general and the generalizable. As a consequence, scientists often consider natural variation an obstacle to be overcome, rather than an end in itself--perhaps at least in part because statistical analyses are difficult when the samples compared have high variances. In the present investigation I have been forced to use a subjective approach to assess uniqueness because more conventional methods greatly underestimate it (Ehrenfeld 1989). The difficulty of quantifying uniqess can be illustrated with the following examples.

Few would deny the contention that the armadillo is an armored animal. But there are many other mammals that have some degree of structural protection. Could not the dermal shields of pigs (Grzimek 1975) or the thick skin of ratels (Carnivora: Mustelidae: Mellivora capensis)(Kingdon 1977) be considered rudimentary armor? Where, then, does one draw the line between armored and unarmored mammals? As another example, star-nosed moles (Condylura cristata) possess a feature that is unique in the strict sense, and we could therefore score them as possessing the feature, and all other species of mammals as lacking it. However, with only n=1 species in the "star-nosed" category, what sort of statistical comparison would be meaningful? Also, there is the problem of comparing attributes--is the armor of an armadillo more or less unusual than the nasal appendages of Condylura?

Most unusual species, however, are only "unique" in that they possess a feature to a greater extent or in a more elaborate form than other species. For these species one would be tempted to somehow rank species as to their degree of possession of a trait. Unfortunately, most species that are unique are unique in many features, some of which are correlated, and it is not obvious which features should be measured or ranked. A precise definition of unusualness would be useful to conservationists and ecologists, but for the moment it can only be assessed subjectively.

To ascertain whether species from monospecific genera are more "unique" I tested whether monospecific genera have more "unique" values for characters than speciose genera. Of course "unique" could be defined in many ways but I preferred to consider only the most obvious features of morphology, behavior and ecology. My method was to list unusual or unique states for characters for each genus, then tally these states for monospecific and speciose genera. The lists I provide for North American (Table 5-1) and Australian (Table 5-2) species are of course arbitrary and subjective but they had the virtue of being simple to compile. I excluded genera that do not have obvious unique values for characters.

Table 5-1. Unusual features of various North American genera of mammals. See text (page 129) for explanation.

Genus	Unusual or Unique Features
Didelphis*	marsupial reproduction; extreme morphological generalism
Microsorex	smallest mammals
Notiosorex*	most xeric-adapted insectivore
Condylura*	unique nasal appendages
Dasypus*	most heavily-armored mammal; polyembryony
Lepus	most cursorial mammals in their size class
Brachylagus*	smallest and most reclusive leporid
Aplodontia*	most primitive rodent; extremely diverse behaviors (burrows, swims, climbs, whistles, constructs nests, "tents" and hay piles)
Eutamias	smallest diurnal rodents
Marmota	by far the largest sciurids
Glaucomys	volplane
Onychomys	most animalivorous cricetid
Castor*	largest rodent; most profound aquatic adaptation; dam building
Baiomys*	smallest rodent
Ondatra*	largest cricetid; flattened tail
Dicrostonyx	in winter, grow bifid claws and turn white
Erethizon*	barbed quills; extreme convergence on ungulate reproductive strategy
Urocyon*	most scansorial canid; most herbivorous canid
Ursus	largest omnivores; only semi-hibernating large Carnivora
Bassariscus*	smallest procyonid; most arboreal nocturnal procyonid
Nasua*	most social of omnivorous carnivores
Martes	most arboreal mustelid
Gulo*	largest home range of any mustelid
Taxidea*	most fossorial mustelid
Lutra*	most aquatic carnivore
Dicotyles*	most omnivorous ungulate; only ungulate without headgear; only non-ruminant ungulate
Alces*	largest cervid; most aquatic cervid

Table 5-1--continued.

Genus	Unusual or Unique Features
Rangifer*	only cervid on arctic tundra
Antilocapra*	extreme cursoriality (e.g., only two digits/foot)
Bison*	largest mammal
Ovibos	only bovid on lowland tundra

* Genus has only one species in North America.

Table 5-2. Unusual features of various Australian genera of mammals. See text (page 129) for explanation.

Genus	Unusual or Unique Features
Tachyglossus*	oviparous; extreme myrmecophagous adaptations; spiny defense
Ornithorhynchus*	oviparous; combination of aquatic/fossorial adaptations; electrical sense in bill to detect prey
Planigale	flattened skull and other features permit prey capture in narrow interstices
Sarcophilus*	carrion-feeding adaptations
Dasyurus	largest predacious dasyurid
Myrmecobius*	termite specialist; diurnal
Thylacinus*	largest predacious marsupial
Notoryctes*	most fossorial insect feeder
Chaeropus*	most cursorial bandicoot
Macrotis	only true burrower among bandicoots
Acrobates*	much smaller than other gliders
Dactylopsila*	woodpecker-like feeding habits
Petauroides*	only folivorous glider
Dendrolagus	only arboreal kangaroos
Bettongia	only macropodids that dig burrows
Hypsiprymnodon*	only quadrupedal, terrestrial macropodid
Tarsipes*	extreme adaptations for flower-feeding
Hydromys*	except for platypus, most aquatic Australian mammal
Mastacomys*	most vole-like rodent (e.g., has broad molars)
Notomys	bipedal saltators

* Monotypic genus.

If the genus possessed values for a character, such as body size, more extreme than other genera in the family or order, it was considered for inclusion in the list, although only if I deemed the difference substantial. However, a slight exaggeration of a trend common to the family was not considered sufficiently "unique". For example, although kangaroo rats (*Dipodomys*) are the heteromyids most highly modified for bipedalism, kangaroo mice (*Microdipodops*) are also frequently bipedal and show many of the same modifications to a lesser degree. As in the previous chapter, I also ignored species not found in North America north of Mexico, thus some of my so-called "monospecific" genera are not strictly monospecific in the taxonomic sense but merely have no congeners in the Nearctic. I did not, however, make a correction for body size as I did for several other analyses. My reasons for this were twofold: 1) Several of the most unusual genera were the smallest in their family or order, and several were the largest; hence, there was no obvious bias; 2) To exclude any genera would have greatly reduced my already small sample size.

I considered only a few genera to be unusual. Scientific specialists could probably name diagnostic characters for every genus; were it otherwise we could not define the genera! However, many of these characters (e.g., penile morphology) are of more interest to a systematist than to an ecologist interested in overall patterns of mammal evolution. Furthermore, as discussed above, a more comprehensive quantitative analysis might be possible but is beyond the scope of this paper.

The hypothesis that monospecific genera are more unusual was tested by comparing the tallies of unique values for characters in monospecific and speciose genera, with the numbers expected for these two types of genera. The expectations were based on the number of species found in monospecific and speciose genera. Thus, since there are more species in the speciose genera, the null model would predict that most of the unique values for characters would be present in the speciose genera. Specifically, since 56.2% of the genera in my North American data set were speciose, the null model predicted that 56.2% of the unique values for characters would be found in speciose genera and 43.8% would be in the monospecific genera. These predicted percentages correspond to 18.8 and 24.2 characters, respectively. This test was then repeated with Australian mammals, with 12.7 and 12.3 characters expected for the speciose and monospecific groups of genera, respectively.

To ascertain whether monospecific genera and speciose genera differ in the same ways as *K*- and *r*- strategists (Prediction 5.3) I tested whether values for variables in living species from monospecific genera differ from those in speciose genera. As discussed earlier, body size was a confounding variable since most of the largest species are found in monospecific genera. To correct for this bias I eliminated all monospecific genera of body size larger than the species *Felis onca*, which is the largest Nearctic species in a speciose genus. Following this criterion I removed the genera *Alces*, *Bison*, *Ovibos* and *Rangifer*. As above, I clarified the comparison by excluding genera with two species. Only living species were used because the data simply are not available for fossil species. I compared species from monospecific genera to species from speciose genera with a Wilcoxon rank-sum test, using a normal approximation and with continuity correction of 0.5. I then replicated the study on Australian mammals.

Results

The mean stratigraphic range of monospecific genera was greater than that of species from speciose genera (Prediction 5.1). The Wilcoxon test I used had a sample size of 536 species, and the SAS computer procedure (SAS Institute 1985) also performted t tests and Kruskal-Wallis tests with Chi-square approximations on the same data. For both the Kruskal-Wallis and t tests, the values were very close to those calculated by the Wilcoxon test. The *P* value of 0.058 was technically nonsignificant at an alpha level of 5%, but the value was very close to 0.05 and could be considered marginally significant.

In my test of Prediction 5.2 the actual number of characteristics in the two types of genera were 31 and 12, a clear reversal of the expected trend. A Chi-square test with Yate's Correction and one degree of freedom produced a Chi-square value of 13.94. This was much larger than the expected value and corresponded to a P value of less than 0.005, so I rejected the null hypothesis of independence of unique values for characters and monospecific status.

The unusual Australian genera are shown in Table 5-2. The expected number of unique characters for monospecific and speciose genera were 12.3 and 12.7, respectively. The observed number of characters for monospecific and speciose genera were 19 and 6, respectively. Thus, although less than half of the extant Australian nonvolant mammal genera are monospecific, approximately three fourths of the unique values for characters belong to monospecific genera; specifically, the Chi-square value with Yate's Correction was 7.16, corresponding to a P value of less than 0.01. Thus, as with North American mammals, Australian monospecific genera have a disproportionate share of unique values for characters.

The results of the test of Prediction 5.3 for North American mammals, are shown in Figs. 5, 2-6. Of the variables tested, litter size, eurytopy, food abundance and heterozygosity were not significantly different between species from monospecific or speciose genera, perhaps because these analyses had small sample sizes. Two

Figure 5-2. Median Wilcoxon ranks for monospecific and speciose genera of North American mammals. The intended contrast is between monospecific and speciose genera, not among variables; the maximum rank for any variable depends upon sample size and has no biological significance. Variables included 1) Head-and-body length; 2) Food abundance (see Table 2-1); and 3) Geographic range size.

North America

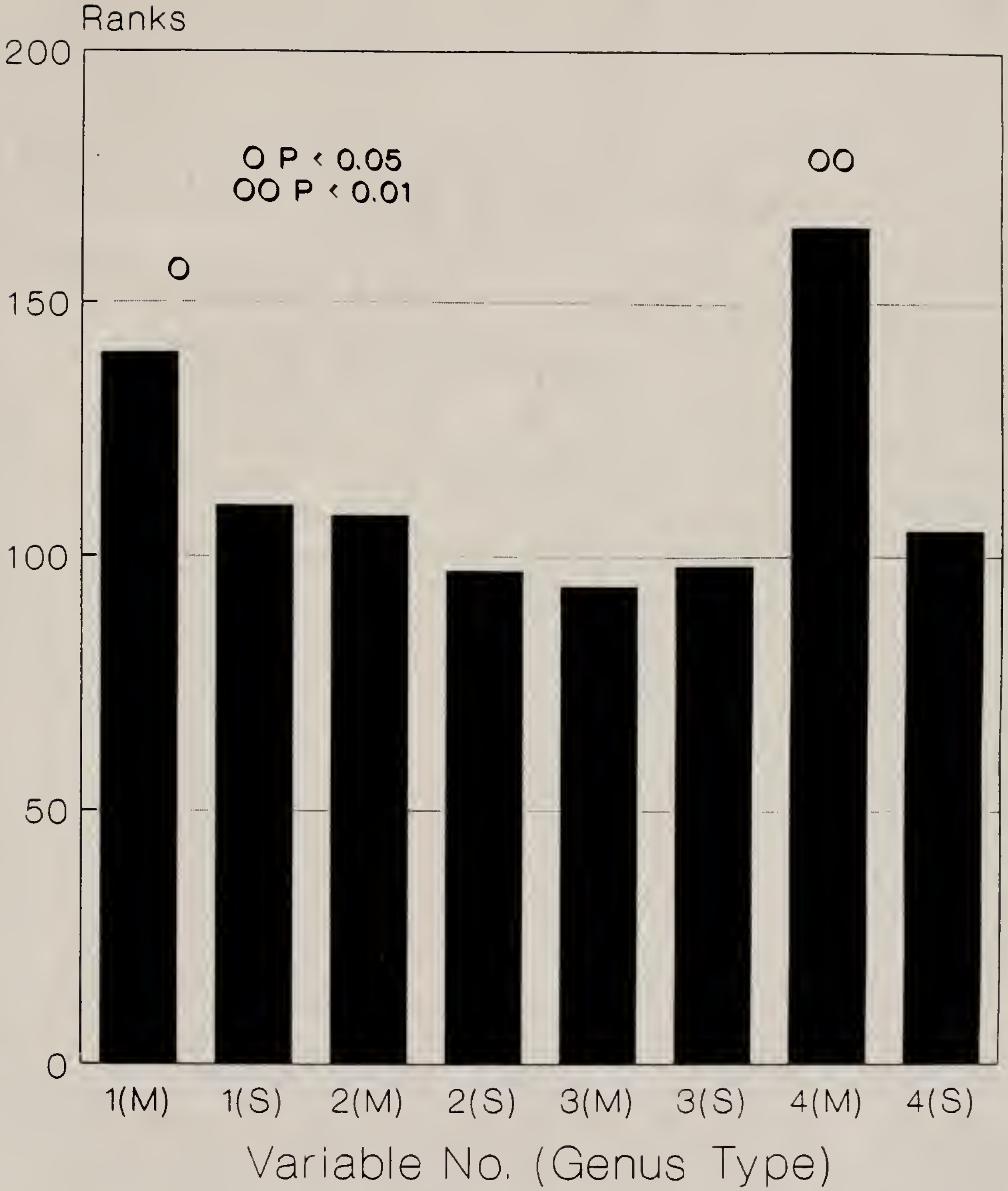


Figure 5-3. Median Wilcoxon ranks for monospecific and speciose genera of North American mammals. The intended contrast is between monospecific and speciose genera, not among variables; the maximum rank for any variable depends upon sample size and has no biological significance. Variables included: 5) Gestation period; 6) Litter size; 7) Population density; and 9) Lactation period.

North America (cont.)

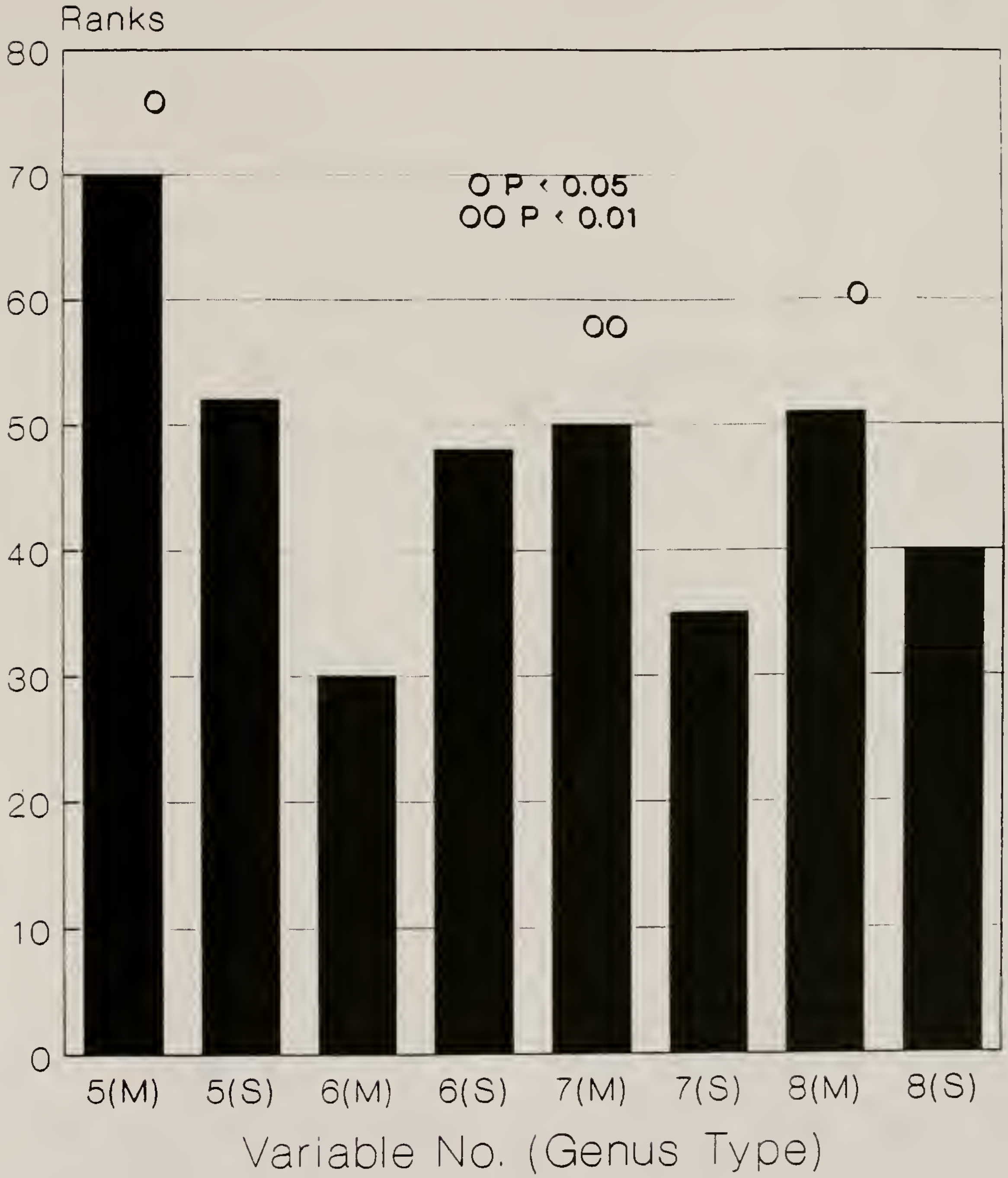


Figure 5-4. Median Wilcoxon ranks for monospecific and speciose genera of North American mammals. The intended contrast is between monospecific and speciose genera, not among variables; the rank for any variable depends upon sample size and has no biological significance. Variables included: 9) Growth rate; and 10) Home range size.

North America (cont.)

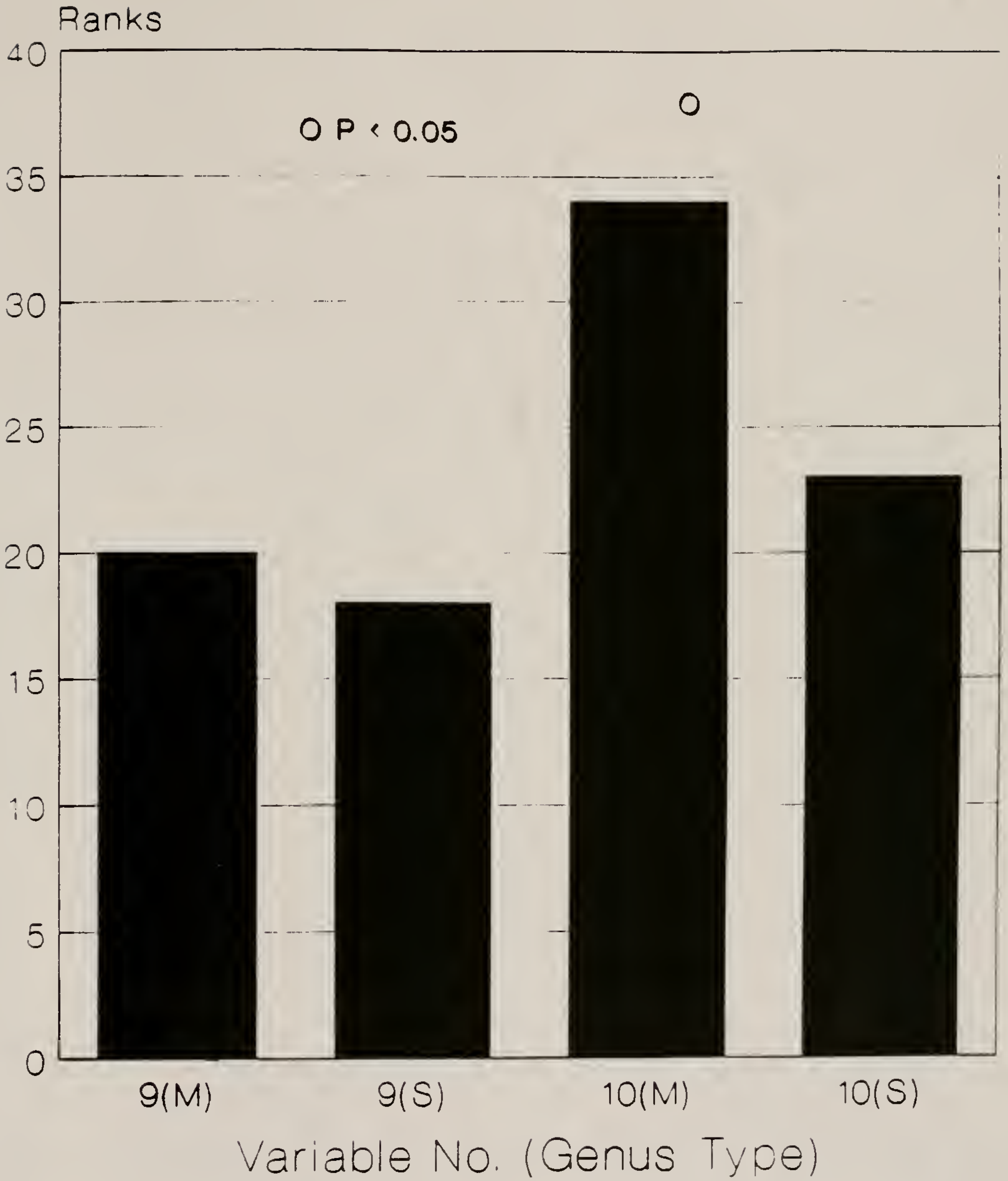


Figure 5-5. Median Wilcoxon ranks for monospecific and speciose genera of Australian mammals. The intended contrast is between monospecific and speciose genera, not among variables; the maximum rank for any variable depends upon sample size and has no biological significance. Variables included: 1) Head-and-body length; and 2) Geographic range size.

Australia

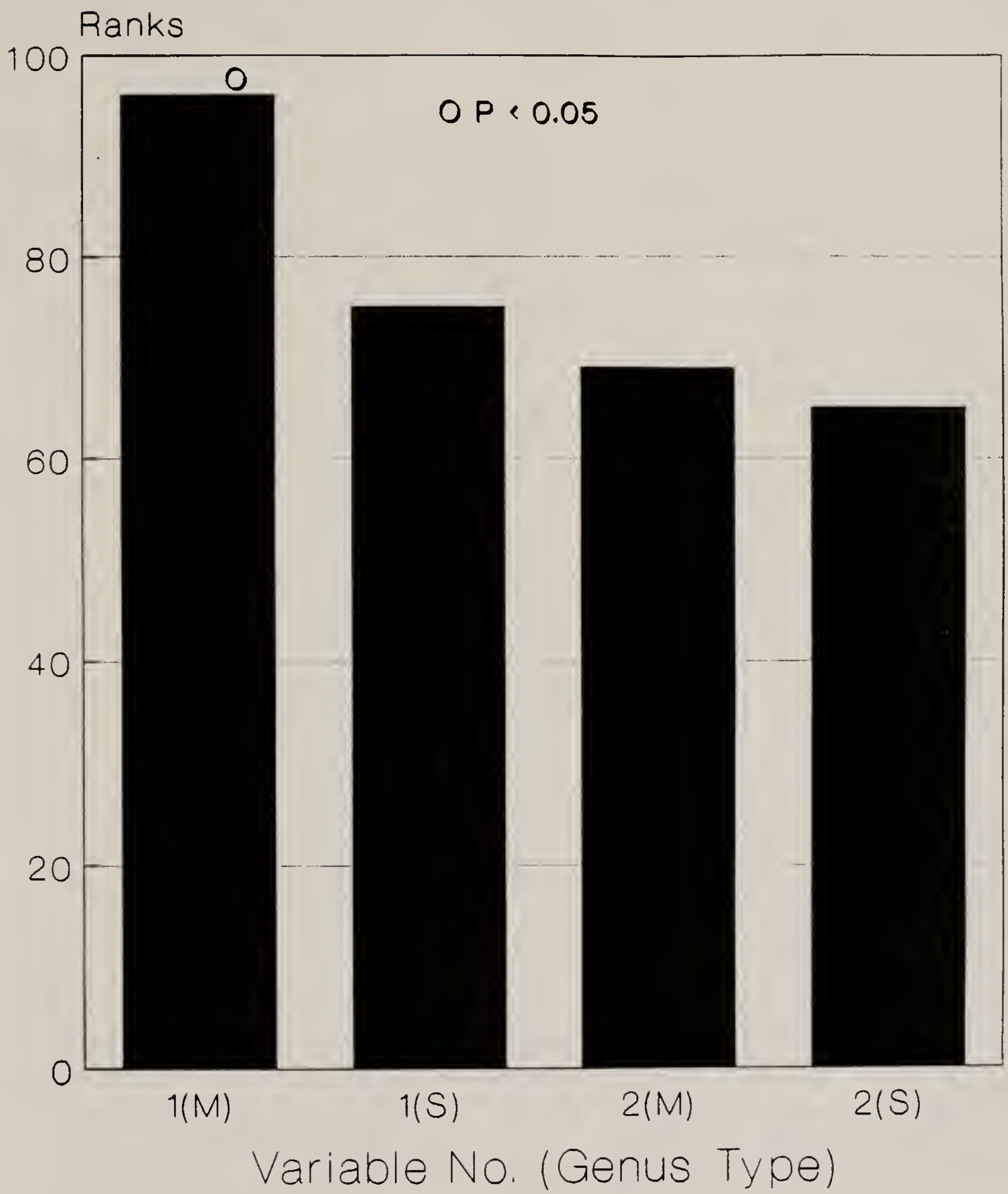
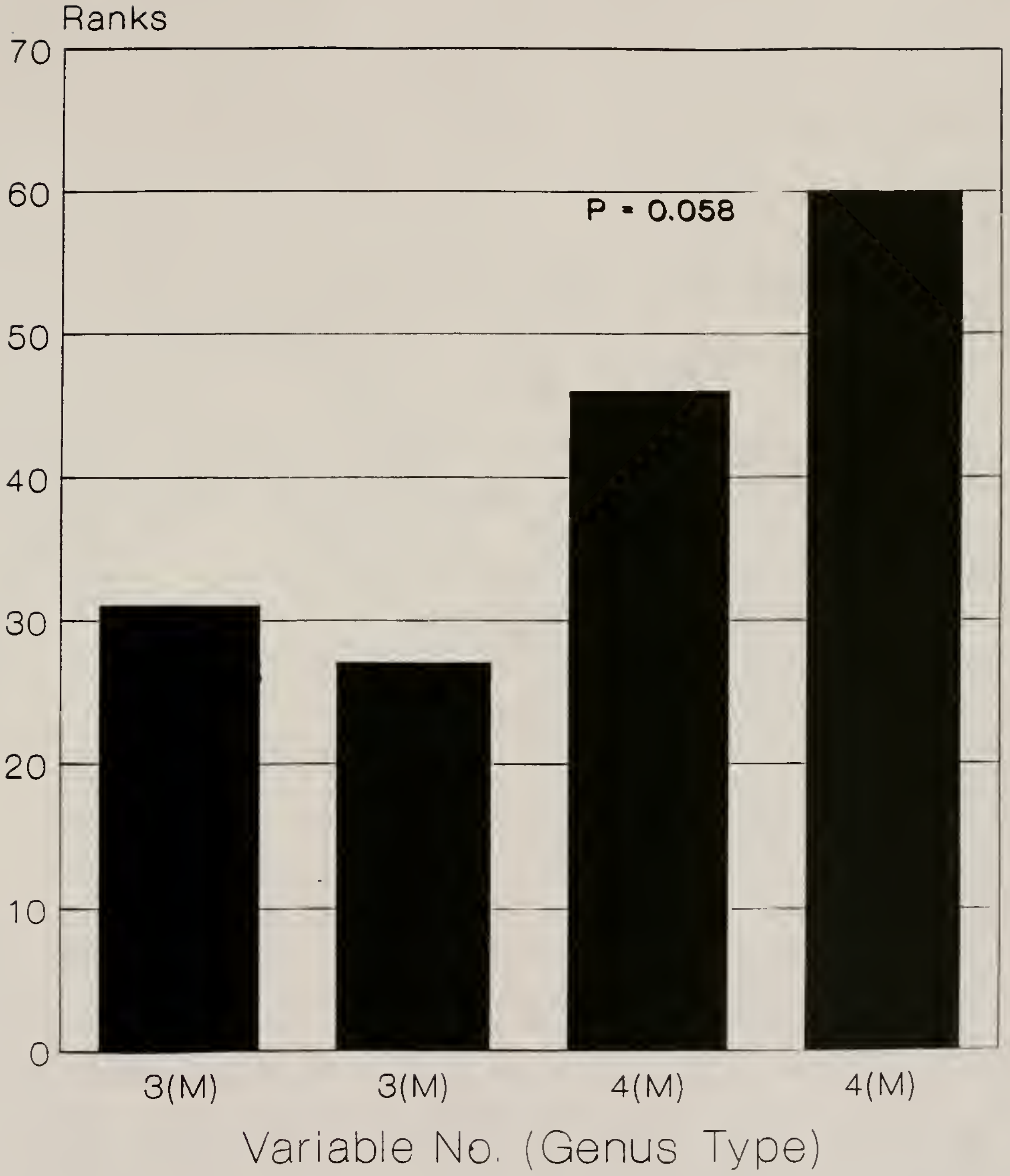

Ranks
100
80
60
40
20
0
O
O P < 0.05
1(M)
1(S)
2(M)
2(S)
Variable No. (Genus Type)

Figure 5-6. Median Wilcoxon ranks for monospecific and speciose genera of Australian mammals. The intended contrast is between monospecific and speciose genera, not among variables; the maximum rank for any variable is dependent upon sample size and has no biological significance. Variables included: 3) Gestation period; and 4) Litter size.

Australia (cont.)



variables, birth weight and growth rate, were very close to being significant, whereas the remaining variables HBL, gestation period, population density, lactation period, RS and home range size differed significantly between the two groups, and HBL was significantly different between monospecific and speciose Australian genera.

Discussion

Although the test of Prediction 5.1 was only marginally significant, I interpret this analysis to support the hypothesis that species from monospecific genera have greater stratigraphic ranges. There is a countervailing trend in extinctions of large species that might tend to reduce the differences between the two groups to a barely-perceptible and only marginally-significant level. One could, for example, hypothesize that body size, which correlates with extinction probability, is the relevant variable. Thus the inverse association between stratigraphic range and numberofspecies per genus could be spurious, and the cause-and-effect relation might actually be between stratigraphic range and body size.

The problem with this explanation is that the association is of the wrong sign. Even if we accept the assumption that large-bodied species have higher extinction rates (but see Pimm *et al*. 1988), we would then predict that species in monospecific genera, being larger, should have a higher extinction rate and thus a smaller stratigraphic range than speciose genera. My data indicate the opposite; species from monospecific genera live longer. The fact that the difference in stratigraphic range between monospecific and speciose genera is only marginally significant could thus be ascribed to selection against species in speciose genera overwhelming selection in favor of small species.

It could also be argued that the greater "unusualness" of monospecific than speciose genera (Prediction 5.2) is an artifact of the methods of systematics. Perhaps systematists have a natural tendency to place the most unusual species in their own (monospecific) genera. I have several responses to this contention.

The first is that much current systematics research is done by means of computerized statistical packages. To the best of my knowledge, the algorithms of these packages are not predisposed to group unusual species into sets of size one, rather than sets of some other size. No doubt these packages are imperfect and sometimes fail to discern true relationships among taxa. However, I am not aware of any evidence that they preferentially cluster unusual species into monospecific rather than dispecific, trispecific, etc., groups. It is possible that classification procedures used by systematists tend to oversplit taxa. If so, however, the bias might tend to separate from the rest the two or three (or more) most unusual species rather than the single most unusual species.

One possible source of evidence for a bias to place unusual species in monospecific genera is the actual distribution of number of species per genus. Unfortunately, the implications of the resulting pattern are unclear. A bias to place unusual species in monospecific genera could be reflected by a preponderance of monospecific genera. However, although monospecific genera are more common than those of any other size, this pattern could also result from evolutionary processes and is consistent with my shotgun model. Furthermore, there is not a disproportionately small number of dispecific genera, as might be expected if species were preferentially placed in genera of size one than in genera of the size most similar to one.

The second reason for believing that the differences between monospecific and speciose genera is not simply an artifact of systematics is that many of the differences are directional, not random. If biased algorithms tend to separate the most unusual species into groups of size one, they should separate from the rest, species with both the largest and smallest values for a character. My comparison revealed that species from monospecific genera differ directionally from species in speciose genera: they tend to be larger in body size and stratigraphic range, to have longer gestations, smaller litters, etc. Thus, if systematic methods are biased to separate unusual species into monospecific genera, they are apparently also biased to separate in monospecific groups only those species that deviate in one sign of polarity and not to separate those of opposite polarity. I am aware of no calculations inherent in statistical procedures that would cause such a bias.

Nevertheless, I have not proved that the differences I found between monospecific and speciose genera are not due to artifact. If systematists actually do have the bias I have discussed, attempts should be made to assess and reduce it. One possibility would be to use standard statistical procedures on the characters of hypothetical species. If the most divergent hypothetical species have been created so as to differ from the others to no greater an extent than these differ from each other, classification algorithms should not be expected to place them in monospecific genera with an unusually high frequency. This test of methodology I leave to systematists.

Several of the significant or nearly significant differences associated with the variables used to test Prediction 5.3 form a correlated suite of characters. Species from monospecific genera were larger even when the four genera of largest body size, which were monospecific, were deleted from the analyses. Not surprisingly, the larger species had longer gestation and lactation periods, greater birth weights, faster growth rates, larger litters, lower densities and larger home range sizes. Obviously to have included the four genera of largest body size would only have inflated an already significant result.

Unfortunately it is difficult to determine whether these differences are meaningful in themselves, or simply inevitable correlates of body size differences; I could, however, rule out trophic strategy (studied as the variable, "food abundance") as a controlling variable because it did not differ significantly between monospecific and speciose genera. Furthermore, the differences in unusualness cannot be entirely attributed to body size differences, because unusual species are to be found in every body size category. Thus body size does not explain all the differences between the two types of genera, although it does explain some of the differences.

Although the tests for several variables revealed no significant differences between monospecific and speciose genera, I consider the overall array of tests to be consistent with my shotgun/logistic model for several reasons: 1) *R*- and *K*- selection theory, as normally interpreted, does not make predictions relevant to some variables in my data set (e.g., food availability). Thus analyses of these variables are irrelevant to the shotgun/logistic model, and were included only for general interest. 2) For every variable shared by the North American and Australian sets of analyses, differences between monospecific and speciose genera were of the same polarity. 3) The Australian data were not all of high quality; hence, there was reason to question the ability of the tests to discriminate between the two types of genera, as follows. RS values for Australian mammals are much less accurate than for North American species not only because Australian mammals have been studied less thoroughly but also because recent extinctions and range reductions have been more prevalent in Australia than in North America (Archer 1984_a_, 1984_b_; Calaby 1984; Watts 1984). In general, gestation periods for North American mammals are explained better by phylogeny than by ecology or local adaptations. Since about half of all Australian mammals are marsupials, and since all marsupials have short gestation periods, the mean and median gestation periods of Australian mammals will be short regardless of ecology. Another Australian variable, abundance, does _not_ refer to population density, but is a subjective interpretation of the commonness of the species. 4) Finally, for several of the tests the sample size was very small, 30 or fewer. For tests involving diverse taxa and much variation, so small a sample is probably inadequate.

My rationale for considering the Australian analyses to support my inferences for the North American analyses is as follows. At least some of the Australian analyses were statistically significant, and these showed differences between monospecific and speciose genera in the same ways as did the North American analyses.

There is yet another reason to implicate higher-level selection as a determinant of the patterns observable in comparisons of monospecific vs. speciose genera. I suggest that the frequency of monospecific genera is much greater than could be explained on the basis of natural selection alone. Speciose genera should, over the vastness of geological time, have greatly outnumbered monospecific genera. This can be demonstrated by a simple model.

Suppose there are three hypothetical species that differ in their propensity for cladogenesis. The first species produces a single chronospecies to replace itself and becomes extinct in the process; each succeeding generation produces exactly one new species to replace itself. The second species produces two daughter species, and each generation continues this trend; likewise for the third species except that it consistently trifurcates into three species. Assuming no extinctions except for the post-reproductive parent species, after just four generations of speciations the first species will result in a single species, the second species will produce 16, and the third, 54 species. Clearly there is a long term evolutionary advantage to prolific cladogenesis and we should therefore expect species from speciose genera to vastly outnumber species from monospecific genera. However, the fact remains that monospecific genera still make up a respectable percentage of the total number of genera. Overall, proneness to speciate and/or to taxonomic longevity must not be passed on to daughter taxa with much fidelity, otherwise monospecific genera would never have been able to overcome the numerical advantages, in terms of numbers of daughter species, of cladogenesis. There is, however, every reason to believe that some species from speciose genera are much more likely than others to undergo cladogenesis (Glazier 1980). Quite simply, many species from speciose genera leave no issue. This, combined with the lower extinction rate for species in monospecific genera, has apparently been enough to maintain a sizable number of monospecific genera. Thus the bulk of the analyses in this chapter are consistent with the shotgun and logistic models proposed in the previous chapter.

I suggest that my analyses of monospecific vs. speciose genera are relevant to the Cenozic as a whole and not just to the Recent. My arguments for this are as follows. For the comparison of stratigraphic ranges of I used a fossil record that stretches back to the Miocene; hence, this is obviously not a phenomenon restricted to the Holocene.

Arguments that my conclusions in the other analyses can be extrapolated to the distant past are somewhat weaker. The strongest support for the generality of the test involving values for several typical variables is that it is consistent with previously-published information. For example, Cope's Law posits long term selection for large body size in a lineage, just as does my own conclusion that species from monospecific genera, as survivors of higher-level selection, are larger than average size for species from speciose genera. By contrast, another possible explanation, predation by early humans, would probably have the opposite effect by selecting against large mammals. Hence, the pattern I discerned occurred despite, not because of, purported human predation.

Although I have no evidence that monospecific genera have always been more unusual than species from speciose genera, I am at a loss to discern any process that could cause a difference between extant and extinct groups in this respect. The usefulness to a star-nosed mole of its tentacles, to a porcupine of its quills, and to an armadillo of its armor are intuitive, and it seems quite reasonable (though untested) to infer that they have influenced the success of these monospecific genera. I can think of no event which would suddenly and generally favor unusual characters when they were not favored before, since the unusual features involved are so diverse. Purported selection pressure by early hunters does not, I believe, explain the success of these creatures; for example, the armor of armadillos and the quills of porcupines are no match for human hunters, who could easily breach such defences with weapons. Hence, recent selection to favor unusual species would, if anything, be weaker than in the early Cenozoic. Thus my analyses probably underestimate rather than overestimate the long-term trend. However, where human-caused extinctions have been particularly severe, as in Pleistocene-to-Recent Australia, the long term patterns may sometimes become too obscure to be readily detected.

Finally, there is other evidence that is consistent with my model if not exactly confirmatory. This concerns the purported inverse correlation between the frequency of species and stratigraphic ranges. My model predicts that speciose genera are made up of many species of short duration, whereas monospecific genera are typically the survivors of speciose genera. We should therefore expect to find a few, long-lived species from monospecific genera, and many short-lived species in speciose genera. A classic paper by Van Valen (1973) presents data consistent with this notion. For many taxa, he plotted logarithms of frequency of surviving taxa (species, genera and families) against their age, and the resulting curves suggest a negative linear function of survivorship with age of taxon. This in itself might seem irrelevant to the present study, but note that a plot of the raw data would not be linear; thus the initially high frequency of taxa drops off exponentially and rapidly to a much smaller frequency of a few, long-lived forms. This is what my model predicts except that I specify that the high frequency is made up of species from speciose genera, whereas monospecific taxa comprise the low frequency of long-term survivors.

CHAPTER VI

DISTURBANCE, INTERCHANGE AND EXTINCTION

Introduction

Periods of great environmental change have been suggested to favor generalized species of invertebrates (Jablonski 1986), as suggested by *r*- and *K*-selection theory. Furthermore, the shotgun/logistic model suggests that species of mammals selected during periods of disturbance will differ from mammals selected over long periods of background extinction, in the same way that *r*-strategists differ from *K*-strategists. Hence, Prediction 6.1 is that species of mammals that are able to expand their geographic ranges during a period of disturbance would therefore be expected to be *r*-strategists relative to species whose ranges remain stable or shrink during disturbance. Furthermore, since disturbance favors colonists, endemics should experience high extinction rates during periods of great environmental change (Prediction 6.2). By contrast, colonist species should make fewer successful incursions into older and climatically stable habitats, where the specializations of the endemic species are seen to their best advantage (Prediction 6.3). With time, however, *K*-selection should eventually transform colonists into specialized endemics (Prediction 6.4). These predictions were assessed without use of elaborate methodology. Hence, a separate section on materials and methods is not included, although Table 6-1 lists the stratigraphic range for certain relevant taxa.

Some Examples and an Assessment of the Predictions

The history of the marsupials is particulary instructive and can illustrate the concepts discussed herein as well as provoking other hypotheses. This is a story based upon Keast (1977), Simpson (1980), Marshall (1982), Archer (1984a,1984b) and upon my own interpretations of modes of selection. I have left out many details and have included only enough information to sketch a basic theme. For example, I will not discuss fossil marsupials from Antarctica, North America or Europe because there have been no adaptive radiations on these continents in the later Cenozoic.

I shall begin this topic by considering the most extravagant radiation of marsupials, that of Australasia. The story begins in the earliest Cenozoic with an isolated Australia that lacks any nonvolant mammals. It should be expected that the first mammals to arrive and proliferate on the land mass would be species adept at colonizing (Carlquist 1974). These colonizing traits are exemplified by didelphid marsupials, which are often small enough to stow away on floating debris or in human ships--indeed, _Marmosa_ opossums still do so today (Lowery 1974; Husson 1978). Most didelphids are also small, prolific and

Table 6-1. Cenozoic stratigraphic ranges of some North American, South American and Australian taxa of mammals.

North America*	
Creodonta and Carnivora	Paleocene to Recent
Titanotheres (Brontotheridae)	Eocene to Oligocene
Perissodactyla	Eocene to Pleistocene
Artiodactyla	Eocene to Recent
Insectivora	Paleocene to Recent
Lagomorpha	Eocene to Recent
Rodentia	Eocene to Recent
South America*	
Marsupialia	Paleocene to Recent
large, carnivorous Marsupialia	Paleocene to Pliocene or Pleistocene
Argyrolagidae	Pliocene to Pleistocene?
Edentata	Paleocene to Recent
Notoungulates and other ungulates	Paleocene to Pleistocene
Astrapotheria	Paleocene to Miocene
Primates	Oligocene to Recent
Caviomorph rodents	Oligocene to Recent
Cricetidae	Pliocene? to Recent
Procyonidae	Miocene to Recent
Mustelidae, Canidae, Felidae, Artiodactyla, Perissodactyla, Lagomorpha, Insectivora, non-caviomorph rodents	Pliocene to Recent
Proboscidea	Pleistocene, or Pliocene to Pleistocene
Australia	
Marsupialia	Paleocene? to Recent
Monotremata	known from Miocene to Recent, but presumed present in Paleocene
Muridae	Miocene or Pliocene to Recent

*Stratigraphic range is not global and applies only to continent under which it is listed. List is not exhaustive and includes only certain examples for the various taxonomic levels.

omnivorous, all ideal traits for a colonizing species. It is not surprising that the first marsupial groups in in Australia were: 1) Didelphids or at least didelphid-like polyprotodonts; and 2) Proto- phalangeroids that resembled didelphids much more than do many extant diprotodont marsupials (Clemens 1977; Kirsch 1977; Dawson 1983) (Incidentally, it does not matter whether marsupials originated elsewhere and then colonized Australia, or the reverse; in either case, the early marsupials on any continent were probably _r_- selected colonists).

Now let us consider the state of the continent itself. If a naturalist were suddenly whisked from the present and transported unawares to pre-marsupial Australia, he or she would probably be perplexed at the lack of mammals. They would no doubt wonder what sort of calamity could have befallen to defaunate so large an area. They would probably suspect that some recent, large-scale disturbance had wiped out the mammal fauna. That is, the mere absence of mammals on a continent-sized land mass would be indicative of disturbance.

I suggest that the early Australian marsupials would have been preadapted to just such a condition and would have reacted to it just as they might have to disturbed, secondary or ecotonal habitats in their continent of origin. The early Australian marsupials apparently proliferated mightily under such circumstances, colonizing the entire land mass, as well as New Guinea, to which Australia has been joined by dry land at various times in the past (Keast 1968; Doutch 1972; Ziegler 1977). Of course in this situation we cannot compare the competive abilities of distubance-adapted and climax-adapted mammals, because only disturbance-adapted species were present. However, we might hypothesize that during periods of environmental stability, a saturated fauna underwent *K*-selection.

Eventually, marsupials colonized all of Australia and saturated the habitats available to them on the continent. Subsequently the evolutionary pressures on many of them shifted from the *r*- selection associated with a colonzing species to the *K*- selection of species in a crowded, stable environment. Natural and higher-level selection then began to weed out the colonizing species in favor of those adapted to a population at equilibrium. Thus we find on the continent today not only *r*-strategists but many *K*-strategists as well, just as among the eutherian mammals on other continents. Examples of such convergence between marsupials and eutherians can be seen in most biology and mammalogy textbooks and will not be discussed here. The similarities between the two groups are by analogy, not homology. For example, large macropodids are very similar in ecology and behavior to various ruminants, but the hopping gait and marsupial mode of reproduction of kangaroos sharply underscore the taxonomic differences between the two groups.

There are, in fact, at least two important ways in which *K*-strategist marsupials differ from *K*-strategist eutherians: the marsupials tend to have longer lactations and shorter gestations. There is considerable overlap in lactation periods between the two groups, so this difference will not be discussed. There is, however, much less overlap in gestation period between marsupials and eutherians of similar size, and in fact for large species there is essentially no overlap (Eisenberg 1981). Marsupials do not seem to be able to prolong intrauterine development as long as eutherians, and thus large marsupials with slow-growing young have had to resort to a prolongation of lactation in an extrauterine environment.

This difference does not gainsay the achievement of some marsupials of a rough functional equivalent of long gestation by a long pouch life. Rather, the point to be made here is that a short gestation is consistent with a colonizing, *r*- selected strategy among mammals, and slavish adherence to it might in some way impede *K*- selection. This potential impediment, or others of which I am unaware, was eventually overcome by the Australian marsupials, which radiated explosively. Apparently with sufficient time and the right selection pressures it is possible to mold extreme *K*-strategists even from such unlikely candidates as didelphid-like marsupials.

Although nonvolant eutherians have not lived in Australia as long as the marsupials, there is some suggestion that they also exhibit a similar tendency, albeit on a smaller scale. The genera of murid rodents that have been in Australia the longest have smaller litters, fewer teats and generally shorter gestation periods than those that have colonized more recently (Watts and Aslin 1981). In other respects, also, the older murids seem more *K*- selected as a whole than the recent immigrants. Hence, Prediction 6.4 is supported.

Marsupials were also present in South America from the very beginning of mammal colonization, and on both continents predaceous forms developed. However on both continents large birds and reptiles shared the role of large predators with the marsupials. This apparent pre-emption was most extreme in South America, where non-marsupials have eclipsed marsupials since the Oligocene Epoch. Nevertheless, some of the predaceous marsupials found in the early Tertiary on the two continents were remarkably similar in morphology and, presumably, habits. An early predisposition toward carnivory might have characterized the early marsupials on both continents. Even the largely herbivorous diprotodont marsupials of Australia occasionally produced more animalivorous lineages (e.g., *Thylacoleo*, *Hypsiprymnodon*, *Dactylopsila*). Note that most of the South American marsupials that did achieve large size and specialized habits were predaceous. Further note that large eutherian predators of the order Carnivora usually have shorter gestations than most other eutherians of similar weight. By contrast, medium- to large-sized herbivores are typically precocial at birth and therefore require a prolonged gestation. I suggest that the long gestation possible for eutherians preadapted them for herbivory. Neotropical marsupials, which lack this preadaptation, developed trophic strategies most compatible with a marsupial mode of reproduction. Among these were the small neotropical marsupials thought to have been ecological counterparts of shrews, moles and small rodents, also animals of short gestation. By and large, it appears that the roles never occupied by neotropical marsupials were roles filled by forms such as ungulates, anteaters, sloths, large caviomorph rodents and monkeys--animals that typically produce precocial young after a long gestation (Kleiman et al. 1979; Eisenberg 1981). Perhaps the longer gestation of eutherians preadapted them as *K*-strategists. As a result, in South America fewer marsupials attained the large size and apparently specialized habits associated with extreme *K*-strategists.

I am not implying that marsupials are inferior competitors in general. The existence in the Neotropics of ecologically diverse marsupial lineages contemporary to eutherians argues against this assertion. I do not, however, preclude a general predisposition for the more plesiomorphic members of each infraclass for a certain range of lifestyles. If early, plesiomorphic members of both infraclasses coexisted, we would expect some divergence to occur as a result both of chance, and more interestingly, because of phylogenetic potential. Thus in South America, where marsupials and eutherians evolved together, marsupials occupied a more limited range of lifestyles, perhaps only those that they were more suited for than the placentals. By contrast, in Australia no such canalization occured, and today we see a wide spectrum of marsupial lifestyles in Australia. Although this line of reasoning would seem to imply a great importance for competition, two caveats should be noted: 1) Eutherians did not drive marsupials to extinction in South America, and the preponderance of eutherians in the neotropics could be an accident of geography. This is because all of the taxa invading South America in the second and third phases of invasion, happen to have been eutherian; 2) Subtle competitive interactions could result in character displacement rather than exclusion or extinction.

This is not to deny that one or the other infraclass might be favored under certain circumstances. Jumping to the level of class, this notion is consistent with the relative importance of predatory mammals and reptiles in Australia as opposed to other continents. Most of the large terrestrial predators in Australia are, and perhaps always have been, non-mammalian. The preponderance of reptiles as top predators in terrestrial Australian ecosystems is not typical of other continents, where mammals usually fill such roles. Even South America, which for a time had a predominance of non-mammals in predatory roles, now has a complement of predators of the order Carnivora. The greater success of reptiles than mammals as top predators during the Cenozoic of Australia has been explained as being due to the differing energy requirements of the two classes, overlaid upon the low productivity of much of Australia (Morton and James 1988). Whatever the reason for the discrepancy between Australia and the rest of the world in this respect, it is clearly an oversimplification that one class is superior to another as top predators, since this varies among continents.

Similarly, it is probably also an overgeneralization that placentals outcompete marsupials. For example, the generally lower metabolic rates and ease of "abortion" of pouch young during periods of resource scarcity might render marsupials competitively superior to predatory placentals in unpredictably arid habitats such as occur over much of Australia. The somewhat more modest success of marsupials in South America could therefore be attributed at least in part to a much smaller extent of unpredictably arid habitat for most of its history, as much as to competition from eutherians. The point I hope to emphasize here and below is that context is extremely important in determining the evolutionary success of a taxon. As Terborgh (1973) pointed out, one of the characteristics of "harsh" habitats is that they cover a relatively small portion of the earth. Note that until recent times desert in southern South America was inhabited by an extremely arid-adapted family of marsupials, the Argyrolagidae. Perhaps if as large a fraction of the neotropics were made up of habitats as low in primary productivity as much of Australia, marsupials would be more abundant in South America.

I have noted that certain taxa of mammals were quite diverse in South America during its long period of isolation. However, many of the South American marsupials became extinct during a period of great biotic tumult at the end of the Tertiary and following the great American biotic interchange between North and South America. Didelphids were the only neotropical marsupials to survive the ensuing mass extinctions in any great numbers. I suggest that the didelphids were already adapted to a lifestyle of colonizing disturbed habitat, and that the great extinctions benefited them by making available more of the ecologically disturbed habitat they had evolved to exploit. Thus at first glance didelphids do not seem to support Prediction 6.4.

Didelphids might, however, support Prediction 6.3. Typical didelphids would not be expected to prosper as well under long term, stable selection in climax, highly productive communities. There are some suggestions that this has been the case. Firstly, tropical didelphids have been noted to reach their greatest densities in disturbed habitats and secondary forest growth, not primary forest (Charles-Dominique 1983). Secondly, those didelphids, such as the genus Caluromys, that have been most successful in primary, undisturbed tropical forest appear to have undergone a shift to K- selection (Eisenberg and Wilson 1981; Charles-Dominique 1983), thus at least in part vindicating Prediction 6.4. It is tempting to think of Caluromys-like didelphids as understudies that could step in at the demise of eutherians to reenact the Australian marsupial radiation.

North America is the third continent with extant marsupials, although these are derived from South or Central American lineages. Only the genus Didelphis has penetrated north of Mexico and I suggest that this genus in particular might exemplify the evolution of extinction-resistance. Although Didelphis would probably be considered r- selected by typical mammalian standards, it is the largest didelphid and might be extinction-resistant simply because it is larger than the other members of its family. Gardner (1973) has suggested that D. virginiana has been the only didelphid to colonize North America because it is tolerant of cold, an application of Bergman's Rule. Perhaps at least part of this tolerance is due to the fact that large animals have larger energy stores than small animals and can probably starve longer (Linstedt and Boyce 1985). Hence, the cold tolerance might be as much starvation-tolerance as anything else. For example, Didelphis is also found with other members of its family in tropical forests. Charles-Dominique (1983) noted that the two largest sympatric didelphids at his study site, Didelphis and Philander, were primarily terrestrial; and hence, were more affected by food shortages than the arboreal species. Perhaps the large body size of these species permits them to fast longer than the smaller species, as suggested for large mammals in general by Lindstedt and Boyce (1985). Furthermore, a species of Didelphis was the more abundant of the only two species of didelphid at a site in northeast Brazil characterized by extreme unpredictability of food (Streilein 1982). A large body size might enable Didelphis to survive from one pulse of food to the next.

Thus Didelphis, which has the largest RS of any genus of didelphid, may outlive most other members of its family simply because its large body size enables it to live in many habitats and thus maintain a large population size. Didelphis might have other characteristics associated with long term survival, at least relative to other didelphids, but information is scanty to test this. It is interesting that the three largest species of didelphids studied by

Charles-Dominique (1983) also have the smallest mean litter of the species studied. Although an inverse correlation between body size and litter size has already been noted for mammals (Eisenberg 1981), it is also what my model would have predicted for a species of large stratigraphic range. Perhaps *Didelphis* (and *Caluromys*?) is in the process of translating short-term ecological success into long-term evolutionary success. Furthermore, if *Didelphis* is typical of mammals, a common first step in achieving greater stratigraphic range might be to slightly increase body size. This assertion might be testable on a finer scale than I used by comparing values for characters of a species that has a large stratigraphic range with those same values for its purported ancestor. If selection for long-term evolutionary success first affects body size then an increase in size will be the most consistent difference between ancestor and descendant for long-lived taxa but not for short-lived taxa.

Given that didelphids are just some of the many disturbance-tolerant species of mammals, it is surprising that I was able to detect as many long-term trends as I did. In a world with so many species spawned by cataclysm and destruction, I consider myself lucky to be able to follow a few threads through the chaos.

It might, however, be possible to follow a few more threads if we look in the right places. The continents of

Africa and Asia are probably good places to begin such a quest for reasons I will describe.

My model suggests that higher-level selection and long-term trends will be most evident during long intervals of environmental stability. Ideally, then, a continent that has experienced no mass extinctions and major perturbations, but which has been subject to a moderate background level of extinctions well-spaced in time, should exhibit more higher-level selection than a biota with few, massive extinctions. Pre-Pleistocene Australia would probably have qualified as a background-level continent, but unfortunately the Pleistocene itself ushered in extensive extinctions on that continent (Martin 1984). Likewise, about half of South America's extant genera of mammals have their ultimate origin in North America of the past three million years (Webb 1985). North America has already been discussed herein, but Africa and Asia remain to be examined relevant to this question. During the Cenozoic there have been many biotic interchanges between Africa and other continents and between Asia and other continents. Hence, at first glance we might expect many pulses of extinction to interrupt higher-level selection. However, because the exchanges were so frequent, each one (except perhaps the first) had relatively less effect than the few that assaulted the Americas and Australia. Presumably if the interchanges occurred frequently enough, they would have very little impact because the biotas being interchanged would be so similar. Thus less biotic disturbance would be predicted for interchanges involving Asia or Africa, the faunas of which are in some sense preadapted for biotic interchange. The much more modest losses of species during the Pleistocene of Africa and Asia than of the Americas and Australia (Martin 1984) bear this out. The relatively greater resistance of African and Asian than South American faunas to higher-level extinction is, however, difficult to fit in the framework of Predictions 6, 1-4 in such a superficial study as this one.

Nevertheless, we could predict that higher-level selection would be more prevalent in Africa and Asia than in Australia and the Americas, since the biota of the former have been more stable. I have not tested this, but the fact that very large, K-strategist mammals are much more speciose in Africa and Asia than in the Americas or Australia is suggestive of long term selection.

Thus the interchanges involving South America were so revolutionary as much because they were so few as because of their magnitude. The first of only two major invasions into an already established South American theriofauna was made up of only two major groups, the caviomorph rodents and the primates. These groups subsequently diversified and became speciose fractions of the fauna, such that the species within them now make up over a quarter of the species and over a third of the genera of the extant, nonvolant mammals of South America (Simpson 1980). However, note that only the second and last of the two major invasions involved a large number of families in several orders, although these groups also underwent diversification. The species derived from this second invasion make up 54% of the genera and 46% of the species of South America. Thus each of the two invasions had far-reaching effects and transformed the fauna in a major way.

By contrast, there have been many interchanges of Africa with Asia, or between these continents and those of Europe and North America, that involved a large number of families of mammals. Generally speaking, throughout much of the latter half of the Cenozoic, the same major groups of mammals were found in Africa, Asia and Europe, and only in recent times have the geographic ranges of some of these (e.g., the Hippopotamidae, Giraffidae and Orycteropidae) contracted to only one or two continents. There has, of course, been considerable faunal turnover on these continents, but on the whole it has tended to occur at lower taxonomic levels than during the two big South American interchanges, and the resulting radiations tended to replace closely related taxa. In South America, however, the newcomers seem often to have exploited new adaptive zones (e.g., Primates). In the instances where newcomers are thought by some to have competed strongly with natives, the invading taxa belonged to different orders or classes (e.g., large rodents vs. native ungulates; Carnivora and phacocorsid birds vs. predatory marsupials). These factors, I believe, are why paleontologists have considered the two South American interchanges to be particularly revolutionary. Rareness of interchange also seems to have rendered the Australian theriofauna especially susceptible to the detrimental effects of invaders. There been more extinctions in the past 200 years in Australia than in North America, and several authorities (for which see Strahan 1983) have specifically implicated invading species as culprits. Also note that the family of mammals to have invaded Australia without the assistance of man, the rodent family Muridae, now makes up over a fifth of the nonvolant mammal species in Australia (Watts and Aslin 1981). I am aware of only one other instance of a single family of invading mammals becoming so large a fraction of a continental theriofauna in such a short period of time. That other instance, the entrance of cricetids into South America, will be discussed below. Note that both of these continents were very isolated from interchange for most of the Cenozoic; hence, the native species possessed few characteristics (e.g., high reproductive rate) especially suitable during an interchange. Predictions 6.1 and 6.2 are supported for Australia and South America.

To expand upon 6.3, I predict (but do not test) that if higher-level selection in Australia and the Americas is anywhere as prevalent as in Africa and Asia, it will be in the oldest, largest, and stablest habitats. I offer this speculation as a potential precursor of future hypotheses.

Similarly, paleontologists studying trends should note that since major biotic changes disrupt long-term species selection, it should be more apparent before a biotic interchange than afterwards. Thus even the continent of South America, which has undergone enormous changes in its mammal fauna in the last three million years, could yet prove instructive in studies of long-term trends and higher-level selection. Note that in this study I have assessed higher-level selection by comparing groups purported to be subject to it with groups purported to be little affected by it. I did something similar for South American mammals by comparing "old native" South Americans, i.e., the taxa whose ancestors were found on the continent before the Panamanian interchange, with those that colonized from the North. South America and Australia were island continents for much of the Cenozoic, undisturbed by biotic invasions from other continents. Thus the mammals found in South America before the interchange and whose extant descendants include edentates, primates, marsupials and caviomorph rodents, might have been subject to uninterrupted higher-level selection, and long-term trends would probably be more apparent among them than among mammals from continents subject to much environmental disturbance. By contrast, the species invading the continent from the north would be disturbance-adapted. This was especially true of the cricetid rodents, the only family of mammalian invaders to achieve a truly explosive radiation in tropical America, and Webb (1985) notes that these cricetids, "...seized new evolutionary opportunities offered by deteriorating climates." In my discusssion of the didelphids, I have already suggested that gestation period might be a major determinant of evolutionary success under certain selective regimes, and I cautiously invoke it again to explain the short term success of the Cricetidae as colonists. Note that not only do the cricetid rodents have the short gestation periods befitting colonists, but that their major potential competitors in South America, the caviomorph rodents, have longer gestation periods. Although these groups might have competed in the past and perhaps still do so today, they probably have reached some sort of taxonomic equilibrium. The caviomorphs apparently reach their greatest species richness in relatively undisturbed and stable habitats and the cricetids in such disturbed habitats as secondary forest, floodplains, high altitudes and agricultural land. Perhaps the most direct evidence for this assertion comes from Lacher and Alho (1989) and O'Connell (1989). The latter study was particularly relevant, because it reported population parameters for caviomorphs and cricetids in two habitats that differed in extent of seasonality and predictability. In the more seasonal of the two habitats, the llanos of Venezuela, no trappable caviomorphs were caught on the study grid. This is what my above generalization predicts for very seasonal habitats, and O'Connell also referred to the cricetids she trapped as 'colonizing species'.

The other habitat, premontane forest, was also seasonal, but less so than the llanos. In this seasonal forest, there was one caviomorph, an echimyid, caught in the traps. As my generalization predicts, this species, Proechimys guairae, had higher survivorship and a lower productivity than the cricetids present. Thus the caviomorph/cricetid dichotomy, and Prediction 6.3, are supported.

I hypothesize that the primary advantage of cricetids over caviomorphs in disturbed habitats is that their shorter gestations (and perhaps larger litters) enable them to produce more individuals in a shorter time to colonize new sites. They are arguably the least endangered neotropical mammals: as of 1982, not a single species of neotropical cricetid was designated as endangered by the International Union for the Conservation of Nature and Natural Resources (IUCN) (Thornback and Jenkins 1982). Admittedly, the IUCN probably does not investigate small rodent endangerment as intensively as it does large mammal endangerment; nevertheless, although some cricetids are probably endangered, the fraction of cricetids with such status is likely to be far less than the fraction of "old native" neotropical mammals that are endangered. Predictions 6.1 and 6.2 are again supported.

There are of course exceptions to these generalizations, but these are few. For example, the capybara (*Hydrochaeris*) has larger litter sizes than might be expected for a large caviomorph rodent. Capybaras, however, are unusual among caviomorph rodents in that they utilize a temporally variable habitat (seasonally flooded grasslands), and in their ability to live in anthropogenic and disturbed habitats (unless eliminated by hunting). One could cautiously invoke a lack of competition to explain the retention or reaquisition of their aberrant, cricetid-like traits: few cricetids have dentition as specialized for herbivory as capybaras, and almost all of them are at least two orders of magnitude smaller in body mass. By contrast, the Chinese water deer *Hydropotes*, which lives in similar habitats and shares certain other features with the capybara, also has a large litter size, in fact the largest of any deer (Nowak and Paradiso 1983)--yet it, like the capybara, retains the long gestation period of its relatives. It appears that the peculiar lifestyle of animals such as the capybara constitute a partial exception to the general rule that caviomorphs have few traits of colonizers.

In general, however, the success of the caviomorphs in stabler habitats is due to adaptations accrued by long-term, higher-level selection. The caviomorph rodents have been in South America since at least the early Oligocene Epoch, whereas the cricetids probably entered in the Pliocene, some 30-35 million years afterwards. Clearly, there has been much more time for long-term trends in the caviomorphs, as evidenced by such specializations as large body size (e.g., Hydrochaeris), fossoriality (Ctenomyidae), cursoriality (Dolichotis), armament (Erethizontidae), etc., and Smythe (1989) provides circumstantial evidence that caviomorph rodents of the family Dasyproctidae have had a long coevolution with the Astrocaryum palms whose seeds they disperse. Yet the oldest caviomorph fossils (e.g., Platypittamys of the family Octodontidae) indicate animals much more generalized in morphology than extant species (Simpson 1980), and it is obvious that the caviomorphs have changed greatly since arriving in South America.

Although the diverse lifestyles of caviomorph rodents might seem to display no common trend, note that in general caviomorph rodents are larger and have longer gestation periods than cricetids, as well as being more highly adapted for herbivory and possessing some specialized antipdredator strategy (e.g., quills, great running speed, escape in water or underground, etc.) Various cricetids possess some of these traits, but usually to much less degree than the caviomorphs. The specialization of the caviomorphs may have come at a cost, and like the other "old native" neotropical mammals, habitat disturbance might make them more vulnerable than the "newcomer" mammals that entered during the interchange.

This is exemplified by the country of Brazil, where, as of 1982, twenty-five species of "old native" mammals (i.e., primates, edentates and caviomorph rodents) were designated as threatened by the IUCN but only twelve of the "newcomer" mammals (i.e., species belonging to lineages that immigrated from North America over the Panamanian land bridge) were so designated (Thornback and Jenkins 1982). Even formerly common caviomorph rodents such as the agouti (Dasyprocta) become rare with only minor habitat alterations (Smythe 1989). Prediction 6.2 is again supported.

Furthermore, a mere tally of the numbers of threatened species probably underemphasizes the fragility of the old natives. All but one of the threatened newcomers is a carnivore, and it just so happens that all the medium- to large-sized predaceous mammals in South America are members of the order Carnivora. Since large vertebrate predators are prime targets for anthropogenic extinction throughout the world, it comes as no surprise that the neotropical Carnivora are threatened. It seems very likely that if large predaceous marsupials had persisted in South America until the Recent that they would be as threatened by humans as are large Carnivora in much of the rest of the world and large carnivorous marsupials (e.g., the thylacine, the Tasmanian devil and the "marsupial lion" Thylacoleo)(Archer 1984c) in Australia. Excluding from consideration medium- and large-sized predators on the grounds that they would be endangered no matter what taxa they belong to, we can calculate that 25 of the 26 or 96.3% of the threatened Brazilian mammals are old natives. In general then, the old natives are probably more sensitive to human disturbance than the newcomer species. This is also consistent with a pattern noted for survivors of North American extinctions; on that continent, a relatively large fraction of the extant megafauna are actually of Eurasian origin--that is, many of the survivors of the changes that occurred at the close of the Pleistocene are invaders (Martin 1984).

Returning again to Australia, my data and general natural history information (e.g., Strahan 1983) suggest that within the family Muridae the ecological characteristics of species support an immigrant/old native dichotomy. The first invasion of murid rodents that colonized Australia, the subfamily Hydromyinae, includes species with more specialized adaptations than the more recently arriving Murinae. Thus it is among the Hydromyinae, not among the Murinae, that are to be found the most aquatic, most xeric-adapted, and most arboreal Australian rodents. Furthermore, the Murinae tend to have higher reproductive rates (and even more teats) than the Hydromyines--as befit colonists. The murines tend to reach much higher densities than the hydromyines in anthropogenic and disturbed habitat, whereas the hydromyines fare less well at such sites, to the extent that some species are endangered by human activities. The murines are usually absent from many natural habitats except during years of rodent plagues, whereas the hydromyines are often present in moderate and less variable numbers. The earliest hydromurines probably resembled murines more than do extant hydromurines; that is, their history could probably be characterized by _K_- selection and specialization. This is consistent with Prediction 6.4. There has probably not been sufficient time, however, for this to happen to murines.

The comparison between "old" and "new" Australian and neotropical rodents can be considered the long-term result of trends that occur even within species; many of the traits that separate "old" and "new" rodents are paralleled by differences between long-established insular populations and more recent, expanding populations (Gliwicz 1980). This is as predicted by _r_- and _K_-selection theory and indicates that the observed differences between endemics and colonists could arise through processes observable in extant species.

Conclusion

The examples presented above are consistent with the hypothesis that biotas subject to frequent biotic interchange and environmental disturbance produce more successful competitors during biotic interchange with other biotas than do biotas that have been subject to fewer disturbances. Conversely, disturbance-adapted species decline in relative importance during periods of background extinction. The general picture that emerges from these investigations is that faunas tend to move along the logistic curve with the passage of time, but that disturbances can "reset the clock" and shift the cumulative character state of the biota back to an *r*-strategist phase. An analogy with ecological succession is almost irresistable: clearly early seral stages differ from the climax stage much as mammals preadapted for great biotic interchange differ from those best suited to long-term stability.

CHAPTER VII

CONCLUSION AND SYNTHESIS

Studies of species extinction have often emphasized the changes in taxonomic composition resulting from extinction events. To a community ecologist, however, it is not so important which names are deleted from the roster, as it is how the loss of species alters natural processes and interactions. Since paleoecology cannot be directly observed, we must look to the patterns resulting from the processes. Fortunately, the patterns of association among many variables are available for study in extant mammals. In the first chapter I showed that nonrandom extinction explained the otherwise anomalous statistical associations among some natural history variables (population density, body size and geographic range size) possessed by North American mammals.

In Chapter II I turned this assumption around. If extinction can explain associations among variables, then should we not be able to use associations among variables to make predictions about extinction? Using data for North American and Australian mammals, I predicted which species not currently designated as threatened with extinction are most likely to become threatened in the near future. This exercise entailed a shift in perspective from the previous chapter inasmuch as it required the acceptance of assumptions and methods that would probably not be considered rigorous enough for conventional science; my justification for such acceptance was that time and resources are not available for methods more acceptable to mainstream science. One of my assumptions was that the population size of a species could be considered a rough indicator of susceptibility to extinction. I then suggested that though population size is rarely known it can be estimated indirectly from the relation, population size = population density times geographic range size. Unfortunately, although RS estimates are possible for almost every North American species, density estimates are available for only a few species. Therefore for the other species I suggested that density be estimated from values for other variables by using known relations of density with other variables.

The ultimate calculations were estimates of population size that were then compared to those for species listed as endangered by the International Union for the Conservation of Nature and Natural Resources. Species that I calculated to be less abundant than those currently designated as endangered were recommended for further investigation. Although this technique is no substitute for field data it does indicate for which species such data is most needed.

In Chapter III I sought more general patterns of nonrandom extinction, patterns that occur over intervals of geologic time. The simple assumptions about extinction that are useful in predicting recent extinctions are not, however, often applicable to the distant past--in part because the data for the relevant variables (e.g., population size and its correlates) are poorly known for fossil species. Fortunately there are theories and testable hypotheses to aid the investigator questing for general patterns of extinction. These theories are not mutually exclusive and there is considerable overlap among them, so in Chapter III I proposed a combination of some of their features into a shotgun/logistic model of adaptive radiation. I suggested that since speciation greatly exceeds extinction during periods of adaptive radiation, and since species selection necessarily involves extinction of species, then it is probably not prevalent during adaptive radiation. However, extinctions follow on the heels of an adaptive radiation and thus species selection should be prevalent after an adaptive radiation.

Furthermore, episodes of species selection tend to follow predictable paths, the aftermaths of which are a few surviving species that differ in predictable ways from the species that perish. Thus assumptions made about evolutionary success are dependent upon which phase of the shotgun continuum are found the taxa investigation: an investigation using data taken from an interval of adaptive radiation could lead one to draw very different conclusions than one using data taken from the following or preceding intervals. *R*- and *K*- selection theory has a place in the shotgun model. At the height of an adaptive radiation, most species will have many of the characteristics of *r*-strategists, whereas the survivors of adaptive radiations resemble *K* strategists.

In Chapters IV and V I examined assumptions about the shotgun model and tested hypotheses whose results would either support or weaken it. The model itself is very broad and difficult to test *in toto*, but I was able to make predictions about differences between monospecific and speciose genera, and among taxonomic levels. In general, the model was supported.

In the final chapter I attempted to improve the accuracy of the model by overlaying it with periods of major disturbance, such as biotic interchange. How, one might ask, do such major perturbations affect the process proposed in the shotgun model? A simplistic answer is that they just "restart the clock" and begin anew the shotgun process. The reality is more complicated and depends upon the context and the taxa involved. Invading taxa often have characteristics associated with the exponential phase of adaptive radiation, as befit colonists. With the passage of time, however, the taxa involved may or may not retain these characteristics. Naturally some taxa will retain the characteristics of a colonist--and these might therefore someday colonize again.

Examples of these include many of the more generalized myomorph rodents, and perhaps the didelphid marsupials.

However with the passage of time and a shift in selection pressures, many colonizing taxa develop different characteristics: they tend to become _K_- strategists, and to develop traits associated with superior competitive ability in a crowded ecosystem. Thus the species that tend to become extinct during a colonizing phase are not necessarily the species that are eliminated by long-term species selection. This is exemplified by South American rodents, of which the "old native" caviomorphs are the better-adapted for life in old and climax habitats, whereas the "newcomer" cricetids prosper in anthropogenic, disturbed and climatically variable habitats. Ecologically, the cricetids probably resemble the earliest caviomorphs; conversely, one could speculate that with time some of the cricetids will come to resemble caviomorphs ecologically. This speculation gains some support from the murid rodents of Australia. On that continent, the oldest murids are _K_- selected relative to the members of the family that have arrived more recently.

In general, then, it is not practical to attempt to place an entire fauna at a certain position along the shotgun/logistic continuum, because not all taxa are at the same position. If this is true, then how can we place a given taxon in its correct position along the continuum?

We can do so in a rough way by making use of a variable well-known to taxonomists and ecologists, namely species richness of the taxon. In Chapter V I found that speciose and monospecific taxa differ in a number of characteristics, most importantly stratigraphic range, that are predicted by the shotgun model. I suggest that the species richness of genera correlates positively with their proximity to the exponential phase of the shotgun/logistic continuum. Most species in speciose genera have a small stratigraphic range as well as traits associated with a colonizing syndrome, and thus could be placed somewhere in the middle or exponential portion of the continuum. By contrast, small or monospecific genera belong at either end of the continuum and are less likely to become extinct soon. This assertion is supported by the fossil record of North American mammals, which shows that the median age for species in monospecific genera is greater than that for speciose genera, and by the disproportionately large fraction of endangered species that belong to speciose genera.

In conclusion, the process of extinction unites theoretical concepts of evolution and ecology with applied conservation. I found that ecological information about extant mammals supported evolutionary theories of extinction. Conversely, an evolutionary framework explained the associations among variables for living species. I used ideas about extinction to predict which extant species might soon be in danger of extinction. Then I turned around and used numbers of endangered species in monospecific and speciose genera to confirm a hypothesis also tested on fossil mammals. By using different types of variables in various comparisons I hope to have avoided much circularity. When fossils, endangered species, island biogeography, body size relations, natural history variables for living species, $\underline{r}$- and $\underline{K}$- selection theory and a variety of other phenomena are all consistent with the shotgun/logistic model, its overall utility is supported. Just as energy has proven useful as a currency that links species in a community, extinction seems to be a currency that the disciplines of evolutionary biology, ecology and conservation can use to deal with each other.

APPENDIX A

DATA FOR NORTH AMERICAN MAMMALS: BIRTH MASS, GEOGRAPHIC RANGE SIZE AND HOME RANGE SIZE

Species	Birth mass[a]	RS[b]	Home range size[c]
Alces alces	18500	279993	1610
Alopex lagopus	-	509592	2080
Ammospermophilus harrisi	-	2680	-
Ammospermophilus interpres	-	2844	-
Ammospermophilus leucurus	-	8529	-
Ammospermophilus nelsoni	-	205	-
Antilocapra americana	3178	54900	1142
Aplodontia rufa	-	2275	-
Baiomys taylori	1.2	9472	-
Bassariscus astutus	28.0	40000	31.5
Bison bison	20000	68157	-
Blarina brevicauda	-	24887	0.43
Brachylagus idahoensis	-	4978	-
Canis latrans	250	116653	619
Canis lupus	-	756445	6250
Canis rufus	-	18618	-
Castor canadensis	500	55824	-
Cervus elaphus	14000	259176	1293
Chaetodipus californicus	1.5	942	-
Chaetodipus penicillatus	-	8889	-
Clethrionomys californicus	-	2074	-
Clethrionomys gapperi	1.9	77331	0.25
Clethrionomys rutilus	-	297610	-
Condylura cristata	-	39600	-
Conepatus mesoleucus	-	22003	-
Cryptotis parva	0.3	41647	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Cynomys gunnisoni	-	3160	-
Cynomys leucurus	-	22909	-
Cynomys ludovicianus	-	14909	1.33
Cynomys parvidens	-	329	-
Dasypus novemcinctus	85.0	138907	-
Dicrostonyx groenlandicus	-	34281	-
Dicrostonyx hudsonius	3.8	60747	-
Dicotyles tajacu	-	125632	135
Didelphis virginiana	-	119467	59.9
Dipodomys agilis	-	766	-
Dipodomys deserti	5.5	3009	-
Dipodomys elator	5.5	437	-
Dipodomys elephantinus	-	17	-
Dipodomys heermani	3.7	1421	-
Dipodomys ingens	-	167	0.05
Dipodomys merriami	3.3	14144	-
Dipodomys microps	-	3644	-
Dipodomys nitratoides	3.3	292	-
Dipodomys ordii	3.3	30200	-
Dipodomys panamintus	4.5	502	-
Dipodomys spectabilis	7.8	4608	-
Dipodomys stephensi	4.4	84	-
Dipodomys venustus	-	128	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Erethizon dorsatum	490	145636	11.3
Eutamias alpinus	-	95	-
Eutamias amoenus	-	10467	-
Eutamias canipes	-	251	-
Eutamias cinereicollis	-	752	-
Eutamias dorsalis	-	6044	0.73
Eutamias merriami	-	809	-
Eutamias minumus	2.5	50688	2.10
Eutamias obeselus	-	145	-
Eutamias ochrogenys	-	84	-
Eutamias palmeri	-	20	-
Eutamias panamintus	-	277	-
Eutamias quadrimaculatus	-	240	-
Eutamias quadrivittatus	3	3594	-
Eutamias ruficaudus	-	1333	6.73
Eutamias senex	-	1136	-
Eutamias siskiyou	-	168	-
Eutamias sonomae	-	399	-
Eutamias speciosus	-	471	-
Eutamias townsendi	3.6	1851	-
Eutamias umbrinus	-	2458	4.55
Felis concolor	450	237644	19365
Felis lynx	204	244931	1852
Felis onca	-	120221	-
Felis pardalis	-	118108	-
Felis rufus	300	88000	2141

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Felis weidi	-	109734	-
Felis yagouaroundi	-	121310	-
Geomys arenarius	-	374	-
Geomys attwateri	-	249	0.01
Geomys bursarius	-	18317	-
Geomys personatus	-	272	-
Geomys pinetus	5.8	2081	-
Glaucomys sabrinus	5.5	74034	-
Glaucomys volans	4.0	38267	-
Gulo gulo	85	369609	40500
Lagurus curtatus	1.5	15104	-
Lemmus sibiricus	3.3	103410	-
Lepus alleni	-	2311	643
Lepus americanus	-	104560	54
Lepus arcticus	-	334891	-
Lepus californicus	-	40356	156
Lepus callotis	-	5333	-
Lepus othus	-	5400	-
Lepus townsendi	95	30400	-
Liomys irroratus	-	5689	-
Lutra canadensis	130	138598	-
Marmota broweri	-	2816	-
Marmota caligata	-	20480	-
Marmota flaviventris	34	16736	1.14
Marmota monax	-	70892	-
Marmota olympus	-	64	-
Martes americana	29	94523	433
Martes pennanti	-	62409	1356
Mephitis macroura	-	17057	-
Mephitis mephitis	-	116942	150
Microdipodops megacephalus	-	2033	-
Microdipodops pallidus	1	263	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Microsorex hoyi	-	2061	-
Microtus californicus	2.8	2926	-
Microtus canicaudus	-	358	-
Microtus chrotorrhinus	-	15950	-
Microtus longicaudus	-	39076	-
Microtus mexicanus	-	9200	-
Microtus miurus	-	11848	-
Microtus montanus	-	13568	-
Microtus ochrogaster	2.9	26054	0.11
Microtus oeconomus	3.0	23696	0.81
Microtus oregoni	1.7	2044	0.02
Microtus pennsylvanicus	2.3	117633	-
Microtus pinetorum	2.1	25388	-
Microtus richardsoni	-	7111	-
Microtus townsendi	-	2120	-
Microtus xanthognathus	-	19800	-
Mustela erminea	1.7	516740	14.0
Mustela frenata	3	124097	112
Mustela nigripes	-	21200	-
Mustela nivalis	1	556410	6.8
Mustela vison	10	150000	270
Napaeozapus insignis	0.9	11800	-
Nasua narica	140	23191	150
Neofiber alleni	12.1	1065	-
Neotoma albigula	-	18015	-
Neotoma cinerea	-	37026	-
Neotoma floridana	11.5	18720	-
Neotoma fuscipes	-	3146	-
Neotoma lepida	-	9827	-
Neotoma mexicana	10	17137	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Neotoma micropus	-	9072	-
Neotoma stephensi	-	2272	-
Neurotrichus gibbsi	0.5	2240	0.41
Notiosorex crawfordi	1.8	22850	-
Ochotona collaris	-	8533	-
Ochotona princeps	-	10667	0.16
Ochrotomys nuttali	2.7	16294	-
Odocoileus hemionus	3630	80789	141
Odocoileus virginianus	2479	133451	180
Ondatra zibethica	25	148099	-
Onychomys arenarius	-	4400	-
Onychomys leucogaster	2.5	35748	-
Onychomys torridus	2.3	13400	-
Oreamnos americana	2950	152000	-
Oryzomys palustris	3.5	28800	-
Ovibos moschatus	11500	22118	-
Ovis canadensis	4150	84942	1433
Ovis dalli	-	16701	-
Pappogeomys castanops	-	7725	-
Parascalops breweri	-	7537	-
Perognathus alticolus	-	89	-
Perognathus amplus	-	1200	-
Perognathus fallax	-	860	-
Perognathus fasciatus	-	8889	-
Perognathus flavescens	-	20139	-
Perognathus flavus	-	13917	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Perognathus formosus	-	3938	-
Perognathus hispidus	-	21600	-
Perognathus inornatus	-	465	-
Perognathus intermedius	-	4622	-
Perognathus longimembris	1.3	2244	-
Perognathus nelsoni	-	5453	-
Perognathus parvus	1.5	8889	-
Perognathus spinatus	-	1022	-
Perognathus xanthonotus	-	44	-
Phenacomys albipes	-	711	-
Phenacomys intermedius	2.1	59620	-
Phenacomys longicaudus	-	748	-
Procyon lotor	67.5	100310	70
Rangifer tarandus	-	263709	-
Reithrodontomys fulvescens	2.0	7289	-
Reithrodontomys humulis	1.0	12788	-
Reithrodontomys megalotis	1.5	48356	-
Reithrodontomys montanus	1.2	17901	-
Reithrodontomys raviventris	-	26	-
Scalopus aquaticus	5.0	31289	-
Scapanus orarius	-	1836	-
Scapanus townsendi	5.0	1027	0.10
Sciurus aberti	12	3009	-
Sciurus arizonensis	-	303	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Sciurus carolinensis	-	35544	0.54
Sciurus griseus	-	3241	0.39
Sciurus nayaritensis	-	2133	-
Sciurus niger	15	36288	-
Sigmodon arizonae	-	3328	-
Sigmodon fulviventer	-	4978	-
Sigmodon hispidus	7.2	122500	0.59
Sigmodon ochrognathus	5.6	1600	-
Sorex arcticus	-	58074	-
Sorex bendirei	-	2178	-
Sorex cinereus	0.28	46077	-
Sorex dispar	-	3200	-
Sorex fumeus	-	7900	-
Sorex gaspensis	-	300	-
Sorex longirostris	-	13200	-
Sorex lyelli	-	433	-
Sorex merriami	-	18400	-
Sorex nanus	-	9600	-
Sorex ornatus	-	1600	-
Sorex pacificus	-	83247	-
Sorex preblei	-	4646	-
Sorex tenellus	-	600	-
Sorex trowbridgii	-	3378	-
Sorex vagrans	0.5	63596	0.11
Spermophilus armatus	-	1742	-
Spermophilus beecheyi	12	4375	0.17
Spermophilus beldingi	-	3067	-
Spermophilus brunneus	-	420	-
Spermophilus columbianus	-	4400	1.4
Spermophilus elegans	6.0	2126	-
Spermophilus franklinii	-	16173	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Spermophilus lateralis	5.0	16438	-
Spermophilus mexicanus	-	7175	-
Spermophilus mohavensis	-	1009	-
Spermophilus parryi	-	68267	-
Spermophilus richardsonii	6.9	11338	-
Spermophilus saturatus	-	822	-
Spermophilus spilosoma	-	13468	-
Spermophilus tereticaudus	-	3189	-
Spermophilus townsendii	-	5200	-
Spermophilus tridecemlineatus	4.0	32497	0.66
Spermophilus variegatus	-	23200	-
Spermophilus washingtoni	-	72	-
Spilogale putorius	9.5	75200	-
Sylvilagus aquaticus	8.9	9041	2.12
Sylvilagus auduboni	-	34133	3.58
Sylvilagus bachmani	27.3	37048	0.28
Sylvilagus floridanus	40	22326	1.62
Sylvilagus nuttalli	-	20400	-
Sylvilagus palustris	-	3208	-
Sylvilagus transitionalis	-	3291	0.46
Synaptomys borealis	-	61779	-
Synaptomys cooperi	3.9	31744	0.05
Tamias striatus	3.0	41842	0.08
Tamiasciurus douglasi	-	4340	-

APPENDIX A--CONTINUED.

Species	Birth mass[a]	RS[b]	Home range size[c]
Tamiasciurus hudsonicus	-	38923	0.49
Taxidea taxus	-	75264	410
Thomomys bulbivorus	6.1	52	-
Thomomys mazama	-	756	-
Thomomys monticola	-	356	-
Thomomys talpoides	-	23880	0.02
Urocyon cinereoargenteus	75	87895	548
Ursus americanus	250	149275	2285
Ursus arctos	681	552876	5310
Vulpes velox	49	3319	1209
Vulpes vulpes	100	744873	-
Zapus hudsonius	0.8	83781	-
Zapus princeps	-	37927	-
Zapus trinotatus	0.8	1915	-

[a] Grams.

[b] Km2 * 10^{-2}.

[c] Hectares.

APPENDIX B

DATA FOR NORTH AMERICAN MAMMALS: HEAD-AND-BODY LENGTH, GESTATION PERIOD, LITTER SIZE AND FOOD ABUNDANCE

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Alces alces	2840	243	1.3	1
Alopex lagopus	600	52	6.8	4
Ammospermophilus harrisi	151	-	6.5	2
Ammospermophilus interpres	228	-	-	-
Ammospermophilus leucurus	217	32.5	7.8	2
Ammospermophilus nelsoni	229	-	-	2
Antilocapra americana	1310	252	2.0	1
Aplodontia rufa	383	-	2.5	1
Baiomys taylori	84.3	20	2.5	3
Bassariscus astutus	349	56	4.0	3
Bison bison	2975	285	1.0	1
Blarina brevicauda	106	21.5	6.5	3
Brachylagus idahoensis	261	-	6.0	1
Canis latrans	850	63	6.0	3
Canis lupus	1125	63	6.0	4
Canis rufus	1098	61.5	4.0	4
Castor canadensis	809	107	3.5	1
Cervus elaphus	2170	247	1.0	1
Chaetodipus cascadensis	84	25	3.0	2
Chaetodipus penicillatus	86.6	23	4.0	2
Clethrionomys californicus	107	-	-	-
Clethrionomys gapperi	100	18	5.0	2
Clethrionomys rutilus	107	-	2.0	2
Condylura cristata	114	45	5.0	3
Conepatus mesoleucus	367	43	3.0	3
Cryptotis parva	61.5	22	5.0	3
Cynomys gunnisoni	282	30	3.0	1.5

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Cynomys leucurus	303	30	5.0	1
Cynomys ludovicianus	280	30.5	5.0	1
Cynomys parvidens	295	-	4.0	1
Dasypus novemcinctus	397	-	4.0	1
Dicrostonyx groenlandicus	129	-	-	-
Dicrostonyx hudsonius	128	20	4.0	1
Dicotyles tajacu	905	145	2.0	1.5
Didelphis virginiana	420	-	8.0	2
Dipodomys agilis	166	-	-	-
Dipodomys deserti	140	30.5	2.0	-
Dipodomys elator	120	-	3.0	2
Dipodomys elephantinus	127	-	-	-
Dipodomys heermani	116	-	3.0	2
Dipodomys ingens	143	-	-	-
Dipodomys merriami	100	28.7	2.0	3
Dipodomys microps	116	-	-	1.5
Dipodomys nitratoides	98	32	2.0	-
Dipodomys ordii	118	29	3.0	2.5
Dipodomys panamintus	131	29	3.0	-
Dipodomys spectabilis	144	-	2.0	2
Dipodomys stephensi	117	-	2.0	-
Dipodomys venustus	116	-	-	-
Erethizon dorsatum	600	210	1.0	1
Eutamias alpinus	101	-	-	-
Eutamias amoenus	120	29	6.0	2
Eutamias canipes	127	-	-	-
Eutamias cinereicollis	131	-	4.0	2
Eutamias dorsalis	127	29.5	5.0	2
Eutamias merriami	131	-	-	-
Eutamias minimus	110	29	5.5	2
Eutamias obeselus	127	-	-	-
Eutamias ochrogenys	148	-	-	-
Eutamias palmeri	131	-	-	-

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Eutamias panamintus	172	-	-	2
Eutamias quadrimaculatus	124	-	-	-
Eutamias quadrivittatus	127	31.5	4.0	2
Eutamias ruficaudus	115	-	-	2
Eutamias senex	140	-	-	-
Eutamias sonomae	141	-	-	3
Eutamias speciosus	127	-	-	2
Eutamias townsendi	137	-	5.0	2
Eutamias umbrinus	125	-	5.0	2
Felis concolor	1373	96	3.0	4
Felis lynx	780	66.5	3.7	4
Felis onca	1422	102	2.0	4
Felis pardalis	863	70	3.0	4
Felis rufus	845	62	3.0	4
Felis weidi	593	-	1.5	4
Felis yagouaroundi	661	67	3.0	4
Geomys arenarius	171	-	5.0	1
Geomys attwatteri	-	-	-	1
Geomys bursarius	202	-	3.5	1
Geomys personatus	184	-	3.2	1
Geomys pinetus	196	-	1.6	1
Glaucomys sabrinus	167	39.5	4.0	2.5
Glaucomys volans	138	40	3.5	2.5
Gulo gulo	850	-	2.9	4.0
Lagurus curtatus	115	25	5.3	1
Lemmus sibiricus	121	23	7.3	1
Lepus alleni	553	-	1.9	1
Lepus americanus	411	36	3.2	1
Lepus arcticus	522	-	6.5	1
Lepus californicus	467	41.5	2.9	1
Lepus callotis	462	-	2.2	1
Lepus othus	549	45	6.4	1
Lepus townsendi	521	42	4.4	1
Liomys irroratus	116	-	4.4	2
Lutra canadensis	732	-	2.6	4
Marmota broweri	421	-	-	1
Marmota caligata	510	-	5.0	1

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Marmota flaviventris	410	30	5.6	1
Marmota monax	414	32	4.3	1
Marmota olympus	599	-	-	1
Martes americana	402	-	2.9	4
Martes pennanti	633	-	2.6	4
Mephitis macroura	287	-	-	2.5
Mephitis mephitis	360	64	6.0	2.5
Microdipodops megacephalus	72	-	3.9	2.5
Microdipodops pallidus	75	-	3.9	2.5
Microsorex hoyi	54.5	-	5.5	3.0
Microtus californicus	132	21	4.7	1
Microtus canicaudus	122	-	3.2	1
Microtus chrotorrhinus	122	-	3.6	1
Microtus longicaudus	186	-	4.5	1
Microtus mexicanus	107	-	2.4	1
Microtus miurus	101	21	6.1	1
Microtus monatanus	116	21	6.0	1
Microtus ochrogaster	119	21	3.7	1
Microtus oeconomus	144	20.3	5.3	1
Microtus oregoni	97	24	3.7	1
Microtus pennsylvanicus	123	21	4.1	1
Microtus pinetorum	104	24	2.3	1
Microtus richardsoni	149	-	6.7	1
Microtus townsendi	137	22	5.1	1
Microtus xanthognathus	157	-	8.4	1
Mustela erminea	137	-	7.5	4
Mustela frenata	254	-	7.5	4

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Mustela nigripes	367	-	3.5	4
Mustela nivalis	159	-	4.5	4
Mustela vison	389	-	4.0	4
Napaeozapus insignis	94	23	5.0	2
Nasua narica	545	77	4.0	2
Neofiber alleni	200	27.5	2.2	1
Neotoma albigula	188	30	2.0	1
Neotoma cinerea	211	35	2.5	1
Neotoma floridana	193	34.5	2.5	2
Neotoma fuscipes	176	-	2.8	1
Neotoma lepida	165	33	2.5	1
Neotoma mexicana	210	32.5	2.2	1
Neotoma micropus	200	33.5	2.5	1
Neotoma stephensi	171	-	1.8	1
Neurotrichus gibbsi	72	-	3.5	3
Notiosorex crawfordi	60.5	-	4.0	3
Ochotona collaris	188	30.0	4.0	1
Ochotona princeps	188	-	4.0	1
Ochrotomys nuttalli	83.0	25.0	2.7	2
Odocoileus hemionus	1474	203	1.6	1
Odocoileus virginianus	1244	211	2.0	1
Ondatra zibethica	288	29	5.1	1
Onychomys arenicola	90.5	-	-	2.5
Onychomys leucopus	103	-	3.5	2.5
Onychomys torridus	94.4	28.5	2.4	2.5
Oreamnos americana	1373	163	1.1	1
Oryzomys palustris	134	25	5.0	1
Ovibos moschatus	2200	246	1.0	1
Ovis canadensis	1476	175	1.0	1
Ovis dalli	1354	-	-	-

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Pappogeomys castanops	193	-	-	1
Parascalops breweri	117	30	4.5	3
Perognathus alticolus	82.5	-	4.2	-
Perognathus amplus	63.0	-	-	2
Perognathus fallax	85.0	-	-	-
Perognathus fasciatus	73.0	28	5	2
Perognathus flavescens	58.0	22.5	4	2
Perognathus flavus	67.0	-	-	2
Perognathus formosus	82.5	-	5.3	2
Perognathus hispidus	113	-	5.5	2.5
Perognathus inornatus	72.5	-	-	-
Perognathus intermedius	76.1	-	3.5	2.5
Perognathus longimembris	59.5	25	3.3	2.5
Perognathus nelsoni	77.0	-	-	2.0
Perognathus parvus	84.2	23	5.3	-
Perognathus spinatus	80.5	-	-	-
Perognathus xanthonotus	85.0	-	-	-
Phenacomys albipes	104	-	-	-
Phenacomys intermedius	108	21.5	5.0	1.5
Phenacomys longicaudus	106	-	-	-
Procyon lotor	525	64	3.5	2
Rangifer tarandus	1855	229	1.0	1
Reithrodontomys fulvescens	72.5	-	3.0	2.5
Reithrodontomys humulis	65.0	21	3.0	2

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Reithrodontomys megalotis	71.9	23	5.0	2
Reithrodontomys montanus	69.8	21	3.0	2
Reithrodontomys raviventris	71.0	-	3.1	2
Scalopus aquaticus	153	43.5	3.5	3
Scapanus latimanus	128	-	-	3
Scapanus orarius	122	-	4.0	3
Scapanus townsendi	170	-	2.9	3
Sciurus aberti	299	42	3.5	2
Sciurus arizonensis	278	44	2.6	2
Sciurus carolinensis	258	46	2.8	2
Sciurus griseus	278	44	2.6	2
Sciurus nayaritensis	276	-	-	2
Sciurus niger	311	44.5	2.8	2
Sigmodon arizonae	158	-	-	-
Sigmodon fulviventer	150	-	-	1
Sigmodon hispidus	144	27	5.6	1
Sigmodon ochrognathus	127	34.5	4.0	1
Sorex alaskanus	84.0	-	-	3
Sorex arcticus	74.2	-	6.4	3
Sorex bendirei	92.0	-	4.0	3
Sorex cinereus	57.8	20.5	7.0	3.5
Sorex dispar	73.0	-	3.5	3
Sorex fumeus	67.6	20.0	5.5	3
Sorex gaspensis	55.3	-	-	3
Sorex longirostris	51.8	-	3.9	3
Sorex lyelli	62.0	-	-	3
Sorex merriami	58.7	-	6.0	3
Sorex nanus	52.6	-	6.5	3
Sorex ornatus	61.9	-	5.0	3
Sorex pacificus	77.5	21.0	6.0	3
Sorex preblei	92.5	-	-	3
Sorex tenellus	52.0	-	-	3

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Sorex trowbridgii	68.5	-	3.5	3
Sorex vagrans	64.7	20.0	5.0	3
Spermophilus armatus	292	28.0	6.0	2
Spermophilus beecheyi	429	30.0	7.0	3
Spermophilus beldingi	205	28.0	6.3	1.5
Spermophilus brunneus	233	-	-	1.5
Spermophilus columbianus	369	-	4.6	2.0
Spermophilus elegans	210	22.5	6.5	2.0
Spermophilus franklinii	247	28.0	7.5	2.0
Spermophilus lateralis	182	28.0	5.3	2.0
Spermophilus mexicanus	175	-	5.0	2.0
Spermophilus mohavensis	220	-	-	-
Spermophilus parryi	348	-	7.2	-
Spermophilus richardsonii	229	23	7.0	2
Spermophilus saturatus	301	-	-	-
Spermophilus spilosoma	152	28	7.0	2
Spermophilus tereticaudus	137	27	6.5	1.5
Spermophilus townsendii	167	-	8.2	1.5
Spermophilus tridecemlineatus	160	27.5	8.5	2.5
Spermophilus variegatus	263	30	4.5	2
Spermophilus washingtoni	215	-	8.0	1.5
Spilogale putorius	197	-	5.0	3.5
Sylvilagus aquaticus	433	37	2.9	1
Sylvilagus auduboni	369	28	3.0	1

APPENDIX B--CONTINUED.

Species	HBL[a]	GEST[b]	LITT[c]	FOOD[d]
Sylvilagus bachmani	317	27	3.5	1
Sylvilagus floridanus	371	29	4.7	1
Sylvilagus nuttalli	325	29	4.5	1
Sylvilagus palustris	403	-	4.0	1
Sylvilagus transitionalis	383	28	4.7	1
Synaptomys borealis	104	-	-	2
Synaptomys cooperi	104	22	3.3	1
Tamias striatus	136	31	4.5	2.5
Tamiasciurus douglasi	179	35	4.0	2
Tamiasciurus hudsonicus	202	35	4.1	2
Taxidea taxus	567	-	3.0	4
Thomomys bulbivorus	210	-	4.2	1
Thomomys mazama	146	28	5.0	1
Thomomys monticola	147	-	-	1
Thomomys talpoides	149	19	5.0	1
Urocyon cinereoargenteus	600	53	4.0	3
Ursus americanus	1420	-	2.5	1.5
Ursus arctos	2000	-	2.2	2
Vulpes velox	454	49	4.5	4
Vulpes vulpes	680	52	4.6	3
Zapus hudsonius	89.5	18	5.5	2
Zapus princeps	88.8	18	5.2	2.5
Zapus trinotatus	93.0	-	6.0	-

[a] Mean head and body length (mm).

[b] Mean gestation length (days).

[c] Mean litter size.

[d] Food Abundance as in Table 2-1.

APPENDIX C

DATA FOR NORTH AMERICAN MAMMALS: LACTATION PERIOD, EURYTOPY AND DENSITY

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Alces alces	-	3	-
Alopex lagopus	-	1	-
Ammospermophilus harrisi	-	2	-
Ammospermophilus leucurus	-	2	0.533
Ammospermophilus nelsoni	-	3	-
Antilocapra americana	-	2	0.019
Aplodontia rufa	-	2	7.7
Baiomys taylori	20.5	1	-
Bassariscus astutus	120	2	0.02
Bison bison	240	4	-
Blarina brevicauda	25	3	10.52
Brachylagus idahoensis	-	1	2.6
Canis latrans	42	4	0.08
Canis lupus	35	4	0.007
Canis rufus	-	4	-
Castor canadensis	42	3	0.102
Cervus elaphus	270	4	-
Chaetodipus cascadensis	23	2	-
Chaetodipus penicillatus	-	4	-
Clethrionomys gapperi	21	4	8.7
Condylura cristata	-	2	-
Conepatus mesoleucus	-	4	-
Cryptotis parva	21.5	4	4.9
Cynomys gunnisoni	21.0	4	-
Cynomys leucurus	-	3	3.2
Cynomys ludovicianus	45.5	3	-

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Cynomys parvidens	-	3	38.2
Dasypus novemcinctus	90.0	-	-
Dicrostonyx hudsonius	16.0	4	-
Dicotyles tajacu	-	4	0.07
Didelphis virginiana	-	4	0.55
Dipodomys deserti	20.0	2	-
Dipodomys elator	20.0	1	-
Dipodomys elephantinus	-	1	-
Dipodomys heermani	21.0	3	-
Dipodomys ingens	-	1	-
Dipodomys merriami	19.5	1.5	-
Dipodomys microps	-	2	-
Dipodomys nitratoides	28.0	1	-
Dipodomys ordii	28.0	4	-
Dipodomys panamintus	28.0	1	-
Dipodomys spectabilis	-	3	-
Dipodomys stephensi	19.0	4	32.4
Dipodomys venustus	14.0	3	-
Erethizon dorsatum	120	4	0.05
Eutamias alpinus	-	2	-
Eutamias amoenus	-	3	-
Eutamias cinereicollis	43	2	-
Eutamias dorsalis	30	2	-

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Eutamias merriami	-	4	-
Eutamias minumus	45	4	24.71
Eutamias panamintus	-	2	-
Eutamias quadrivittatus	46	-	-
Eutamias speciosus	-	1	-
Eutamias townsendi	-	4	-
Eutamias umbrinus	-	2	-
Felis concolor	42	4	-
Felis lynx	-	2	0.005
Felis onca	-	4	-
Felis pardalis	-	4	-
Felis rufus	60	4	0.005
Felis weidi	-	4	-
Felis yagouaroundi	-	4	-
Geomys arenarius	-	3	-
Geomys bursarius	45	4	-
Geomys personatus	-	2	-
Geomys pinetus	30	3	-
Glaucomys sabrinus	60	4	5.5
Glaucomys volans	49	2	7.0
Gulo gulo	-	2	-
Lagurus curtatus	21	2	0.45
Lepus alleni	-	4	0.35
Lepus americanus	30	4	-
Lepus arcticus	-	4	1.2
Lepus californicus	21	1	-
Lepus callotis	-	1	-
Lepus othus	-	4	0.06
Lepus townsendi	-	3	-
Liomys irroratus	-	3	-
Lutra canadensis	95	3	0.01
Marmota caligata	-	1	0.4

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Marmota flaviventris	30	1	-
Marmota monax	45	3	13.5
Marmota olympus	-	1	-
Martes americana	42	3	0.01
Martes pennanti	70	4	0.057
Mephitis macroura	-	3	-
Mephitis mephitis	49	4	0.05
Microdipodops megacephalus	-	3	-
Microdipodops pallidus	-	3	-
Microsorex hoyi	-	3	0.52
Microtus californicus	-	-	108
Microtus longicaudus	-	-	22.0
Microtus mexicanus	-	-	32.5
Microtus ochrogaster	21	-	35.5
Microtus oregoni	-	-	19.5
Microtus pennsylvanicus	12.5	-	105.5
Microtus pinetorum	17	-	-
Microtus townsendi	-	-	166.5
Mustela erminea	67	4	0.04
Mustela frenata	-	4	0.07
Mustela nigripes	-	1	-
Mustela nivalis	-	4	0.05
Mustela vison	38.5	3	0.059
Napaeozapus insignis	34	2	-
Nasua narica	120	3	0.26
Neofiber alleni	-	2	-
Neotoma albigula	30	3	-
Neotoma cinerea	-	2	2.7
Neotoma floridana	30	4	-
Neotoma fuscipes	21	4	-
Neotoma lepida	-	3	-

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Neotoma mexicana	-	1	-
Neotoma stephensi	-	1	-
Neurotrichus gibbsi	-	4	-
Notiosorex crawfordi	-	3	23.7
Ochotona collaris	-	2	6.8
Ochotona princeps	-	3	-
Ochrotomys nuttali	21	3	12.3
Odocoileus hemionus	-	4	1.3
Odocoileus virginianus	-	4	0.03
Ondatra zibethica	30	3	16.4
Onychomys leucogaster	28	4	-
Onychomys torridus	20	3	1.8
Oreamnos americana	-	2	-
Oryzomys palustris	16	3	2.9
Ovibos moschatus	-	4	-
Parascalops breweri	-	3	-
Perognathus amplus	-	4	-
Perognathus fallax	-	2	-
Perognathus fasciatus	-	3	1.5
Perognathus flavescens	30	3	-
Perognathus formosus	-	3	-
Perognathus hispidus	-	4	-
Perognathus inornatus	-	3	-
Perognathus intermedius	-	3	38.5
Perognathus longimembris	16	3	-

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Perognathus parvus	-	4	-
Perognathus spinatus	-	4	-
Perognathus xanthonotus	-	4	-
Phenacomys albipes	-	3	-
Phenacomys intermedius	-	4	4.9
Phenacomys longicaudus	-	3	-
Procyon lotor	70	3	0.2
Rangifer tarandus	-	3	-
Reithrodontomys fulvescens	14.5	4	-
Reithrodontomys humulis	21	3	6.18
Reithrodontomys megalotis	20	3	-
Reithrodontomys montanus	14	4	-
Reithrodontomys raviventris	-	2	-
Scalopus aquaticus	-	3	-
Scapanus latimanus	-	3	-
Scapanus orarius	-	4	-
Scapanus townsendi	-	2	-
Sciurus aberti	133	1	4.5
Sciurus arizonensis	-	3	4.3
Sciurus carolinensis	60	4	2.4
Sciurus griseus	-	2	4.3
Sciurus nayaritensis	-	1	-
Sciurus niger	-	4	1.9
Sigmodon arizonae	-	3	-
Sigmodon fulviventer	-	4	-

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Sigmodon hispidus	20	4	22.2
Sigmodon ochrognathus	-	1	-
Sorex arcticus	-	3	8.56
Sorex bendirei	-	3	-
Sorex cinereus	-	4	14.0
Sorex dispar	-	1	-
Sorex fumeus	-	4	-
Sorex gaspensis	-	1	-
Sorex longirostris	-	4	-
Sorex lyelli	-	4	-
Sorex merriami	-	1	-
Sorex nanus	-	3	-
Sorex ornatus	-	2	-
Sorex pacificus	-	3	-
Sorex preblei	-	3	-
Sorex tenellus	-	3	-
Sorex trowbridgii	-	3	-
Sorex vagrans	25	4	-
Spermophilus armatus	-	2	23.0
Spermophilus beecheyi	-	4	20.1
Spermophilus beldingi	-	2	43.9
Spermophilus brunneus	-	1	-
Spermophilus columbianus	-	4	12.2
Spermophilus elegans	35	3	8.9
Spermophilus franklinii	-	3	14.8
Spermophilus lateralis	-	2	-
Spermophilus mexicanus	-	4	-
Spermophilus mohavensis	-	2	-
Spermophilus parryi	20	3	3
Spermophilus richardsonii	-	3	3.1

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Spermophilus saturatus	-	2	-
Spermophilus spilosoma	-	4	5.0
Spermophilus tereticaudus	-	4	22.6
Spermophilus townsendii	-	1	17.5
Spermophilus tridecemlineatus	30	4	12.2
Spermophilus variegatus	56	3	6.9
Spermophilus washingtoni	-	4	-
Spilogale putorius	56	3	0.055
Sylvilagus aquaticus	-	3	0.41
Sylvilagus auduboni	24.5	4	4.83
Sylvilagus bachmani	-	2	-
Sylvilagus floridanus	31.5	4	9.0
Sylvilagus nuttalli	-	4	-
Sylvilagus palustris	-	3	-
Sylvilagus transitionalis	16	4	-
Synaptomys borealis	-	3	-
Synaptomys cooperi	21	3	8.0
Tamias striatus	30	3	27.18
Tamiasciurus douglasi	-	2	-
Tamiasciurus hudsonicus	70	2	3.18
Taxidea taxus	60	4	0.0279
Thomomys bulbivorus	42	4	-
Thomomys mazama	-	4	-
Thomomys monticola	-	2	-
Thomomys talpoides	40	4	16.1

APPENDIX C--CONTINUED.

Species[a]	Lactation[b]	Eurytopy[c]	Density[d]
Urocyon cinereoargenteus	70	4	0.017
Ursus americanus	-	4	0.005
Ursus arctos	-	4	0.000
Vulpes velox	44	4	-
Vulpes vulpes	-	4	0.025
Zapus hudsonius	28	3	6.9
Zapus princeps	30	-	-
Zapus trinotatus	-	3	-

[a] Not listed are species for which data are lacking for all three variables.

[b] Days.

[c] Eurytopy as in Table 2-1.

[d] Number of individuals per hectare.

APPENDIX D

DATA FOR NORTH AMERICAN MAMMALS: GENIC HETEROZYGOSITY, GROWTH RATE AND GENIC POLYMORPHISM

Species[a]	Hetero[b]	Growth Rate[c]	Poly[d]
Alces alces	0.02	390	0.158
Ammospermophilus leucurus	-	0.69	-
Antilocapra americana	0.01	-	0.053
Aplodontia rufa	-	4.88	-
Baiomys taylori	-	0.15	-
Bassariscus astutus	-	4.9	-
Bison bison	0.023	-	0.053
Canis latrans	-	49	-
Canis lupus	-	160	-
Cervus elaphus	0.015	-	0.104
Chaetodipus californicus	-	0.48	-
Cryptotis parva	-	24	-
Cynomys ludovicianus	-	3.43	-
Didelphis virginiana	0.01	1.25	-
Dipodomys agilis	0.04	-	0.11
Dipodomys deserti	0.01	-	0.06
Dipodomys elator	0.02	-	0.0
Dipodomys merriami	0.051	0.43	0.16
Dipodomys microps	0.007	-	0.03
Dipodomys nitratoides	0.04	0.55	0.22
Dipodomys ordii	0.08	-	0.03
Dipodomys panamintus	0.0	-	0.0
Dipodomys spectabilis	0.008	-	0.06
Erethizon dorsatum	-	21.2	-
Eutamias minimus	0.06	-	-
Geomys arenarius	0.05	-	0.12
Lepus americanus	-	13.1	-
Lepus californicus	-	16.8	-

APPENDIX D--CONTINUED.

Species[a]	Hetero[b]	Growth Rate[c]	Poly[d]
Lepus townsendi	-	21	-
Lutra canadensis	-	25	-
Marmota flaviventris	0.05	-	-
Mephitis mephitis	-	7.9	-
Microtus californicus	-	0.98	-
Microtus oeconomus	-	0.79	-
Microtus pinetorum	-	0.8	-
Mustela nivalis	-	0.86	-
Nasua narica	-	11.3	-
Neotoma lepida	-	0.9	-
Ochotona princeps	0.47	-	-
Odocoileus hemionus	0.05	240	0.105
Odocoileus virginianus	0.07	244	0.358
Ovibos moschatus	-	365	-
Ovis canadensis	-	143	-
Perognathus longimembris	-	0.25	-
Phenacomys longicaudus	-	0.4	-
Procyon lotor	0.01	-	-
Rangifer tarandus	0.01	347	0.0
Sciurus arizonensis	0.029	-	0.09
Sigmodon hispidus	0.021	1.07	0.08
Spermophilus beecheyi	-	3.3	-
Spermophilus beldingi	-	3.59	-
Spermophilus franklinii	-	3.6	-
Spermophilus lateralis	-	1.98	-
Spermophilus richardsonii	-	3.5	-

APPENDIX D--CONTINUED.

Species[a]	Hetero[b]	Growth Rate[c]	Poly[d]
Spermophilus spilosoma	-	0.54	-
Spermophilus tereticaudus	-	1.73	-
Spermophilus townsendii	-	-	-
Spermophilus tridecemlineatus	-	1.1	-
Sylvilagus aquaticus	-	11.1	-
Tamias striatus	-	0.84	-
Tamiasciurus hudsonicus	-	1.5	-
Thomomys talpoides	0.046	-	0.233
Ursus americanus	-	96	-
Vulpes velox	-	20	-
Vulpes vulpes	0.0	30	-

[a] Not listed are species for which data was not available for all three variables.

[b] Genic heterozygosity.

[c] Grams/day.

[d] Genic polymorphism.

APPENDIX E

DATA FOR AUSTRALIAN MAMMALS: GEOGRAPHIC RANGE SIZE, HEAD-AND-BODY LENGTH AND LITTER SIZE

Species	RS[a]	HBL[b]	LITTER[c]
Acrobates pygmaeus	12000	73	-
Aepyprymnos rufescens	10000	385	1
Antechinomys laniger	28000	85	-
Antechinus apicalis	460	69	7
Antechinus bellus	770	126	9
Antechinus flavipes	6900	113	11
Antechinus godmani	77	133	5
Antechinus leo	154	130	9
Antechinus minimus	740	115	3
Antechinus rosamondae	1540	101	8
Antechinus stuartii	2300	96	-
Antechinus swainsonii	2300	122	8
Antechinus sp. (Ningbing)	770	90	-
Bettongia gaimardi	3800	323	1
Bettongia lesueur	39000	372	1
Bettongia penicillata	12000	330	1.1
Burramys parvus	77	108	4
Caloprymnus campestris	770	268	-
Cercartetus caudatus	310	106	2.5
Cercartetus concinnus	6200	81	-
Cercartetus lepidus	770	64	4
Cercartetus nanus	3100	91	4
Chaeropus ecaudatus	15400	245	2
Conilurus albipes	5400	-	-
Conilurus penicillatus	3100	-	2
Dactylopsila trivirgata	770	263	-
Dasycercus cristicauda	17000	160	7
Dasyuroides byrnei	3800	158	-
Dasyurus geoffroyii	36000	326	6
Dasyurus hallucatus	13000	215	6
Dasyurus maculatus	5400	484	5
Dasyurus viverrinus	4600	363	6

APPENDIX E--CONTINUED.

Species	RS[a]	HBL[b]	LITTER[c]
Dendrolagus bennettianus	77	-	1
Dendrolagus lumholtzi	154	-	1
Echymipera rufescens	154	350	-
Gymnobelideus leadbeateri	310	160	1.5
Hemibelideus lemuroides	154	330	1
Hydromys chrysogaster	32000	300	3.5
Hypsiprymnodon moschatus	154	232	2
Isoodon auratus	18000	232	3
Isoodon macrourus	6900	375	3
Isoodon obesulus	4600	315	3
Lagorchestes asomatus	310	-	-
Lagorchestes conspicillatus	19000	435	1
Lagorchestes hirsutus	18000	353	1
Lagorchestes leporides	5400	450	-
Lagostrophus fasciatus	2300	430	1
Lasiorhinus krefftii	770	-	-
Lasiorhinus latifrons	460	-	1
Leggadina forresti	19000	90	3.5
Leporillus apicalis	20000	-	-
Leporillus conditor	9200	-	-
Macropus agilis	6200	725	1
Macropus antilopinus	5400	-	1
Macropus bernardus	154	665	1
Macropus dorsalis	5400	1338	1
Macropus eugenii	770	615	1
Macropus fuliginosus	14600	801	1
Macropus giganteus	18000	-	1
Macropus greyi	6200	-	1
Macropus irma	1540	1200	1
Macropus parma	310	496	1
Macropus parryi	4600	840	1
Macropus robustus	64000	519	1
Macropus rufogriseus	6900	798	1
Macropus rufus	48000	-	1
Macrotis lagotis	49000	383	-
Mastacomys fuscus	770	161	2

APPENDIX E--CONTINUED.

Species	RS[a]	HBL[b]	LITTER[c]
Melomys sp.	770	125	-
Melomys burtoni	3100	131	2.5
Melomys capensis	460	130	-
Melomys cervinipes	154	78	2
Mesembriomys gouldii	3100	-	2
Mesembriomys macrourus	5400	-	1.5
Myrmecobius fasciatus	15400	245	-
Ningaui timealeyi	2300	52	5.5
Notomys alexis	29000	102	3.5
Notomys amplus	154	143	-
Notomys aquilo	310	102	-
Notomys cervinus	2300	110	3
Notomys fuscus	2300	105	3
Notomys longicaudatus	154	125	-
Notomys mitchelli	5400	115	3.5
Notomys mordax	620	-	-
Notoryctes typhlops	14000	140	-
Onychogalea fraenata	9200	543	-
Onychogalea lunata	4600	140	-
Onychogalea unguifera	11000	585	-
Ornithorhynchus anatinus	4600	460	2
Parantechinus bilarni	310	79	4.5
Perameles bouganville	14000	240	2
Perameles eremiana	7700	255	2
Perameles gunnii	310	305	2.5
Perameles nasuta	5100	368	2.5
Petauroides volans	6900	400	1
Petaurus australis	3800	200	1
Petaurus breviceps	23000	170	2
Petaurus norfolcensis	8470	210	2
Petrogale brachyotis	3800	480	1
Petrogale burbidgei	154	322	1
Petrogale inornata	1540	485	1
Petrogale lateralis	11000	505	1
Petrogale penicillata	3100	520	1
Petrogale persephone	77	580	1
Petrogale rothschildi	1540	525	1
Petrogale xanthopus	1540	590	1
Phalanger maculatus	460	-	3
Phalanger orientalis	154	-	2

APPENDIX E--CONTINUED.

Species	RS[a]	HBL[b]	LITTER[c]
Phascogale calura	1540	-	8
Phascogale tapoatafa	11000	-	8
Phascolarctos cinereus	16000	749	1
Planigale gilesi	9200	72	7
Planigale ingrami	4600	59	8
Planigale maculatus	5400	80	8
Planigale tenuirostris	12000	64	-
Pogonomys mollipilosus	310	138	2.5
Potorous longipes	154	400	1
Potorous platyops	310	243	-
Potorous tridactylus	770	360	1
Pseudocheirus archeri	154	100	1
Pseudocheirus dahli	1540	360	1
Pseudocheirus herbertensis	154	349	2
Pseudocheirus peregrinus	14000	325	2
Pseudomys albocinereus	3100	77	4
Pseudomys apodemoides	400	75	4
Pseudomys australis	7700	135	3.5
Pseudomys chapmani	620	60	-
Pseudomys delicatulus	17000	65	3
Pseudomys desertor	12000	92	3
Pseudomys fieldi	770	104	-
Pseudomys fumeus	770	90	3.5
Pseudomys gouldii	6200	115	-
Pseudomys gracilicaudatus	3100	126	3
Pseudomys hermannsburgensis	29000	75	3.5
Pseudomys higginsi	310	133	3.5
Pseudomys nanus	4600	100	3
Pseudomys novaehollandiae	620	78	4
Pseudomys occidentalis	154	97	-
Pseudomys oralis	2300	150	-
Pseudomys pilligaensis	77	71	-
Pseudomys praeconis	154	100	3.5
Pseudomys shortridgei	1540	110	-
Rattus colletti	620	132	-
Rattus fuscipes	3800	165	5

APPENDIX E--CONTINUED.

Species	RS[a]	HBL[b]	LITTER[c]
Rattus leucopus	460	170	3.5
Rattus lutreolus	3100	164	4
Rattus sordidus	2300	165	6
Rattus tunneyi	18000	147	4
Rattus villosissimus	24000	177	-
Sarcophilus harrisii	620	611	4
Setonix brachyurus	770	478	1
Sminthopsis butleri	460	88	-
Sminthopsis crassicaudata	32000	75	9
Sminthopsis douglasi	460	-	-
Sminthopsis granulipes	1540	83	-
Sminthopsis hirtipes	11000	77	-
Sminthopsis leucopus	1540	96	9
Sminthopsis longicaudata	10000	88	-
Sminthopsis macroura	39000	85	8
Sminthopsis murina	15400	84	9
Sminthopsis ooldea	5400	72	7.5
Sminthopsis psammophila	154	102	-
Sminthopsis virginiae	3100	98	8
Tachyglossus aculeatus	77000	375	1
Tarsipes rostratus	3100	96	2.5
Thylacinus cynocephalus	620	1150	-
Thylogale billardieri	1540	595	-
Thylogale stigmatica	1540	478	-
Thylogale thetis	770	470	-
Trichosurus arnhemensis	13000	410	-
Trichosurus caninus	3100	450	1
Trichosurus vulpecula	27000	-	1
Uromys caudimaculatus	770	317	2.5
Vombatus ursinus	3800	985	1.1
Wallabia bicolor	10000	727	1
Wyulda squamicaudata	620	400	1
Xeromys myoides	310	121	-
Zyzomys argurus	8470	93	2.5

APPENDIX E--CONTINUED.

Species	RS[a]	HBL[b]	LITTER[c]
Zyzomys pedunculatus	1540	125	-
Zyzomys woodwardi	1540	143	-

[a] $Km^2 \times 10^{-2}$.

[b] Millimeters.

[c] Mean litter size.

APPENDIX F

DATA FOR AUSTRALIAN MAMMALS: DENSITY, LACATION PERIOD AND HOME RANGE SIZE

Species[a]	DENSITY[b]	WEAN[c]	HRS[d]
Acrobates pygmaeus	15	93	-
Aepyprymnos rufescens	0.07	-	-
Antechinus flavipes	-	90	-
Antechinus stuartii	2.11	-	-
Bettongia gaimardi	-	155	-
Burramys parvus	2.6	60	-
Cercartetus caudatus	-	80	-
Cercartetus concinnus	-	50	-
Cercartetus nanus	-	65	-
Conilurus penicillatus	-	20	-
Dasycercus cristicauda	-	105	-
Dasyuroides byrnei	-	110	-
Dasyurus hallucatus	-	150	-
Dasyurus viverrinus	-	171	-
Gymnobelideus leadbeateri	-	-	1.5
Hydromys chrysogaster	-	28	-
Isoodon macrourus	-	60	3.5
Isoodon obesulus	-	65	7
Lagostrophus fasciatus	-	270	-
Macropus agilis	-	330	-
Macropus fuliginosus	1.22	-	-
Macropus parma	-	294	-
Macropus parryi	0.5	450	-
Macropus robustus	0.065	380	-
Macropus rufogriseus	4.26	435	65
Mastacomys fuscus	-	35	-
Melomys burtoni	-	21	-
Melomys capensis	-	-	-
Melomys cervinipes	0.55	20	-
Myrmecobius fasciatus	-	-	100
Ningaui timealeyi	-	90	-
Notomys cervinus	-	28	-
Notomys fuscus	-	30	-
Notomys mitchelli	-	35	-
Perameles gunnii	8.5	-	-
Perameles nasuta	-	60	-
Petauroides volans	2.8	-	-
Petaurus breviceps	4.7	130	0.55

APPENDIX F--CONTINUED.

Species[a]	DENSITY[b]	WEAN[c]	HRS[d]
Phascolarctos cinereus	-	365	-
Planigale gilesi	-	90	-
Planigale maculatus	-	70	-
Planigale tenuirostris	-	95	-
Pseudocheirus peregrinus	-	180	-
Pseudomys albocinereus	2.5	-	-
Pseudomys gracilicaudatus	6	28	0.5
Pseudomys novaehollandiae	17	-	-
Pseudomys praeconis	-	30	-
Rattus fuscipes	0.9	-	-
Rattus leucopus	-	25	-
Rattus lutreolus	2.2	-	1.22
Sarcophilus harrisii	-	210	15
Sminthopsis butleri	-	70	-
Sminthopsis crassicaudata	0.9	-	-
Sminthopsis leucopus	4	-	-
Sminthopsis macroura	-	70	-
Sminthopsis murina	-	65	-
Tachyglossus aculeatus	-	65	-
Tarsipes rostratus	-	90	-
Thylogale billardieri	-	170	-
Thylogale thetis	-	180	-
Trichosurus arnhemensis	3	165	1
Trichosurus caninus	0.1	270	-
Uromys caudimaculatus	-	56	-
Vombatus ursinus	0.3	-	14
Wallabia bicolor	0.63	450	-

[a] Not listed are species for which data is lacking for all three variables.

[b] Number of individuals per hectare.

[c] Length of lactation in days.

[d] Home range size in hectares.

APPENDIX G

CALCULATING POPULATION SIZES OF NORTH AMERICAN MAMMALS

The following is a description of how a portion of a SAS computer program was used to calculate population sizes for North American mammals using the regression equation Log density = $-0.26692\ HBL^{.5} + 5.01300$.

Since the equation calls for the variable HBL to be transformed, the first step was a transformation. Thus the command:

$HBL50 = HBL^{.5}$;

was used. Since the computer reads one asterisk as multiplication and two asterisks as exponentiation, the equation in the program read:

LogDENS = $-0.26692 * HBL^{.5} + 5.01300$;

However, the calculation estimates log density, not density, hence I employed a command to calculate the antilog of the log density, thus:

```
NDENS = 2.71828 ** LDENS;
```

Calculation of population size entailed a multiplication of RS times density. I could not, however, calculate population size unless the two variables used similar units for area. Therefore, since the density values in my data set were in hectares, but my RS data were in km^2, I needed to multiply my densities by 100:

```
KDENS = NDENS * 100;
```

Furthermore, since RS in km2 is typically very large, the RS values in my data set were expressed as km^2 times 10^{-2}. Therefore to calculate the actual RS I needed to multiply my RS values by 100:

```
NRS = RS * 100;
```

The final command necessary to actually estimate population size was thus:

```
POP = KDENS * NRS;
```

APPENDIX G--CONTINUED.

A "PROC PRINT" command then instructed the computer to print the data, as well as the values for HBL50, LDENS, NDENS, KDENS, NRS and POP.

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